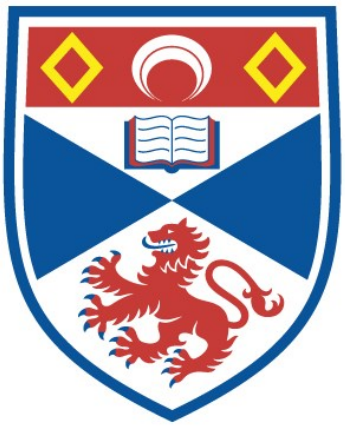
PARASITOLOGICAL STUDIES

Michael David Brunskill Burt

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



1967

PARASITOLOGICAL STUDIES

Part I Identification and description of avian cestodes from Borneo.

Part II Investigation into the problem of host specificity by means of experimental infestation.

being a Thesis presented

by

Michael David Brunskill Burt

to the

University of St. Andrews

in application for the degree of

Doctor of Philosophy

Fredericton, 1967.

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DECLARATION

I hereby declare that the following thesis is my own composition, is based on observation and experimental work carried out by me, and has not been presented for a Higher Degree.

Michael D. B. Burt

RESEARCH TRAINING

My training in Parasitological research started during my honours year, 1960-61, in the University of St Andrews. During that year I worked on a research problem under the supervision of Mr. Ian M. Sandeman, the results of this work being published the following year.

During the year 1961-62 I held the temporary appointment of Assistant Professor in the Department of Biology, University of New Brunswick where I supervised research by an honours student, M. Keith Pomeroy, on the cestodes of herring gulls. This work was completed by me in 1963 and published jointly the following year.

Parasitological Studies, as presented in this thesis, started on June 1, 1962, under University Court Ordinance LXXIX (St Andrews No. 16). The work was started in McGill University, Canada, where I spent the summer of 1962 as Assistant to Professor T. W. M. Cameron, Director of the Institute of Parasitology, Macdonald College, McGill University, Montreal. From October, 1962 to September, 1964 I continued with this research in St Andrews under the supervision of Mr. D. R. R. Burt. I joined the permanent staff of the University of New Brunswick as Assistant Professor in the Department of Biology in September, 1964 where I completed my research work and wrote this thesis.

The results of some of the research carried out by me, alone and in collaboration, are as follows:

BURT, M. D. B. 1962. A contribution to the knowledge of the Cestode Genus Ophryocotyle Friis, 1870. J. Linn. Soc.-Zoology, 44, (301), 645-668.

POMEROY, M. K. and BURT, M. D. B. 1964. Cestodes of the herring gull, Larus argentatus Pontoppidan, 1763, from New Brunswick, Canada. Can. J. Zool., 42, 959-973.

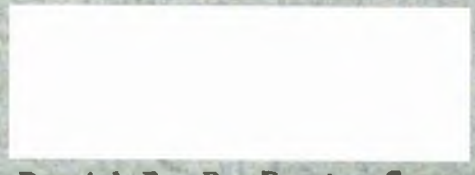
DICK, T. A. and BURT, M. D. B. 1967. Some observations on the life cycle of Davainea tetraoensis Fuhrmann, 1919. Can. J. Zool., 45, (in press).

BURT, M. D. B. 1967. On the ultrastructure of Diplocotyle (Pseudophyllidea:Cyathocephalidae). Parasitology, (in press).

DICK, T. A. and BURT, M. D. B. 1967. Seasonal variation in Davainea tetraoensis, a cestode parasite of ruffed grouse. Parasitology, (in press).

CERTIFICATE

I hereby certify that Michael David Brunskill Burt was admitted as a Research Student in the Department of Natural History, University of St. Andrews on June 1st, 1962. He has spent nine terms on research on Parasitology, has fulfilled the conditions of Ordinance No. 16 (St. Andrews) and is qualified to submit the following thesis in application for the degree of Doctor of Philosophy.



David R. R. Burt, Supervisor.

ACKNOWLEDGEMENTS

In addition to the help already acknowledged throughout the thesis, I should like here to express my sincere thanks to Professor H.G. Callan for allowing me to undertake the bulk of my research in the Department of Natural History, the University of St. Andrews and also to Professor C.W. Argue who provided me with facilities and constant encouragement in the Department of Biology, University of New Brunswick where this thesis was written. I should like to thank also, Dr. T.W.M. Cameron for providing the initial research problem and the facilities of the Institute of Parasitology, Macdonald College, McGill University, Professor J.G. Baer who so kindly spent much of his valuable time discussing many of the problems associated with the first part of this thesis, and Mr. S. Prudhoe for making available the material in the British Museum (Natural History) and for his kindness and advice on many occasions.

Grateful acknowledgement is also made to the Department of Scientific and Industrial Research and to Madras College Trustees who awarded me research grants to work in the Department of Natural History, the University of St. Andrews, and to the British Council who awarded

me a Scholarship making it possible to spend part of the summer, 1963, in the Institut de Zoologie, Université de Neuchâtel, under the direction of Professor Baer.

I should like to thank also Professor J.C. Buckley who provided me with the type material of Raillietina bodkini Vevers, 1923; Mr. D.R.R. Burt who provided me with the type material of Paricterotaenia tringae Burt, 1940 and Notopentorchis collocaliae Burt, 1938; Mr. H. Ferguson who so kindly gave me a clutch of Japanese quail eggs which were hatched and used in some of the infestation experiments; Mr. G.N. Bance and Miss C.P. McCaffrey for assistance with the photography done for the thesis; the reference staffs of the libraries of St. Andrews University and of the University of New Brunswick whose work in procuring required literature is greatly appreciated; and Mrs. C.M. Harris and Miss M.E. Elder for their careful typing of the manuscript and for their continued patience.

Finally, above all, I should also like to acknowledge, with deep gratitude, the supervision, help, and constant encouragement of Mr. D.R.R. Burt, late Senior Lecturer in the Department of Natural History, the University of St. Andrews.

CONTENTS

INTRODUCTION

The following thesis consists of two main sections. In Part I avian cestodes from Borneo are identified and described, and the synonymy and systematic problems associated with each species are discussed. Part II describes experimental attempts made to elucidate one of the problems which constantly faces systematists, namely, that of being able to recognize inter-specific differences as opposed to intra-specific variation.

The collection of cestodes from Borneo was made by a team of workers in the United States Navy Medical Corps under the supervision of Dr. R. E. Kuntz. Animals belonging to all the vertebrate classes were brought to the temporary research stations which Dr. Kuntz had established in Borneo and were there examined for all parasites. As a consultant to the United States Navy, Professor T. W. M. Cameron - late Director of the Institute of Parasitology, Macdonald College, McGill University - was entrusted with the task of having much of the collection identified. As I had arranged to start work towards the degree of Doctor of Philosophy of St. Andrews University under the initial direction of Professor Cameron, it was suggested by him that I undertake the identification of the cestodes from Borneo. This topic

was approved by my supervisor in St. Andrews, Mr. D.R.R. Burt, who suggested further that I carry out such experimental work as might be suggested by problems arising from the systematic survey of these cestodes.

In carrying out the identification and description of the cestodes from Borneo, type specimens of as many relevant species as possible were examined for purposes of comparison and correct identification. Most of the type specimens required are housed in the collection of Professor Jean G. Baer, Institut de Zoologie, Université de Neuchâtel and it was through the kindness of The British Council in awarding me a scholarship under the Younger Research Workers Interchange Scheme that I was able to spend part of the summer of 1963 working in Neuchâtel under the direction of Professor Baer. A few of the type specimens required are in the British Museum and through the kindness of D.S.I.R. and the courtesy of Mr. S. Prudhoe who is in charge of the Platyhelminth Section of the Museum, I was able to examine the type material there. Much of the work on cestodes in the Far East has been done by Mr. D.R.R. Burt, my supervisor, who very kindly placed his entire collection, including type material, at my disposal. Wherever possible, original descriptions were studied and these became avail-

able through the diligent application and generous co-operation of the staff of St. Andrews University Library who ferreted out from innumerable and diverse sources the articles and journals required.

The problem of recognizing such differences as might exist between two worms as: (1) being simply variation within a single species (intra-specific variation); or (2) representing differences which serve to separate two distinct species (inter-specific differences), has always been paramount in systematic work and was no less so in the present studies. Throughout the two-year period of identifying and describing the cestodes from Borneo it became increasingly obvious that in many cases the only differentiating feature between two separate species was some character which often exhibited wide variation within some other single species. It seemed, then, a reasonable hypothesis that perhaps different species of host could provide a parasite with environments which might differ sufficiently to cause a slight modification in the size or shape of some morphological character. Taking the hypothesis further, it did not seem unreasonable to suspect that two hosts of the same species, but living apart geographically with perhaps associated nutritional and climatic differences, could also provide environments

which were sufficiently different to cause slight morphological differences in otherwise identical parasites. Evidence relating to specific examples is discussed which illustrates how two hosts of different species appear to have affected differently the morphological development of the cestodes infesting them. Similarly there can also be seen instances of zoogeographical variation of apparently the same cestode species.

From the above observations it seemed worthwhile investigating experimentally, by artificial infestation, whether hosts of separate species might affect differently the morphological development of cestodes of the same species infesting them. As most of the evidence that this might happen had been drawn from the survey of avian cestodes, it was decided initially to use birds as experimental hosts. The preface to Part II introduces more fully the various experimental infestations tried and the hosts and parasites used.

TECHNIQUES

Fixing:

The collection of avian cestodes from Borneo had been fixed by Dr. R. E. Kuntz and his team as soon as possible after the death of the host. Unfortunately as some of the birds examined for parasites had been dead for as long as several days, not all the tapeworms recovered were in a good enough state of preservation to allow for identification. After receiving the collection from Dr. T. W. M. Cameron, all the cestodes were washed thoroughly, over several days, in three changes of 70 per cent alcohol and were then stored in fresh 70 per cent alcohol.

Staining and sectioning:

Worms to be mounted whole were stained either in Ehrlich's haematoxylin or in acetic acid alum carmine. Ehrlich's haematoxylin was used at full strength and the worms were allowed to become heavily over-stained. They were then differentiated in one per cent hydrochloric acid in 70 per cent alcohol, "blued" in one per cent ammonium hydroxide in 70 per cent alcohol, dehydrated, cleared in cedar wood oil, and mounted in Canada balsam or Permount. Acetic acid alum carmine was found to be particularly

useful in staining small worms and was used as a progressive stain. Worms were initially hydrated and washed overnight in distilled water before being placed in a dilute solution of the stain in water (five drops of stain in 50 cc of distilled water) for one or two days. After staining, the worms were dehydrated, cleared, and mounted as before.

Wherever possible, portions of worms were embedded in paraffin wax for sectioning and the rest of each worm from which the portions had been cut was stained and mounted whole as previously described. Horizontal sections were cut at 15μ and transverse sections were cut at 5-10μ. Sections were stained in Ehrlich's haematoxylin and counter-stained in eosin.

Examination of rostellar hooks, sucker spines, and oncosphere hooks was facilitated by using Berlese fluid. Scolices and gravid proglottides, wherever possible, were squashed in a drop of Berlese fluid on a slide. This technique renders most tissue transparent and thus allows for more accurate measurement of hooks which are pressed into a horizontal position. The true shape of the hooks is also more readily seen and this allows for greater accuracy in drawing.

Drawings:

All drawings were made using a Wild drawing tube mounted on a Wild M 20 research microscope.

PART I

IDENTIFICATION AND DESCRIPTION OF AVIAN CESTODES FROM BORNEO

Paronia bocki Schmelz, 1941

Host: *Megalaima chrysopogon* 8891*

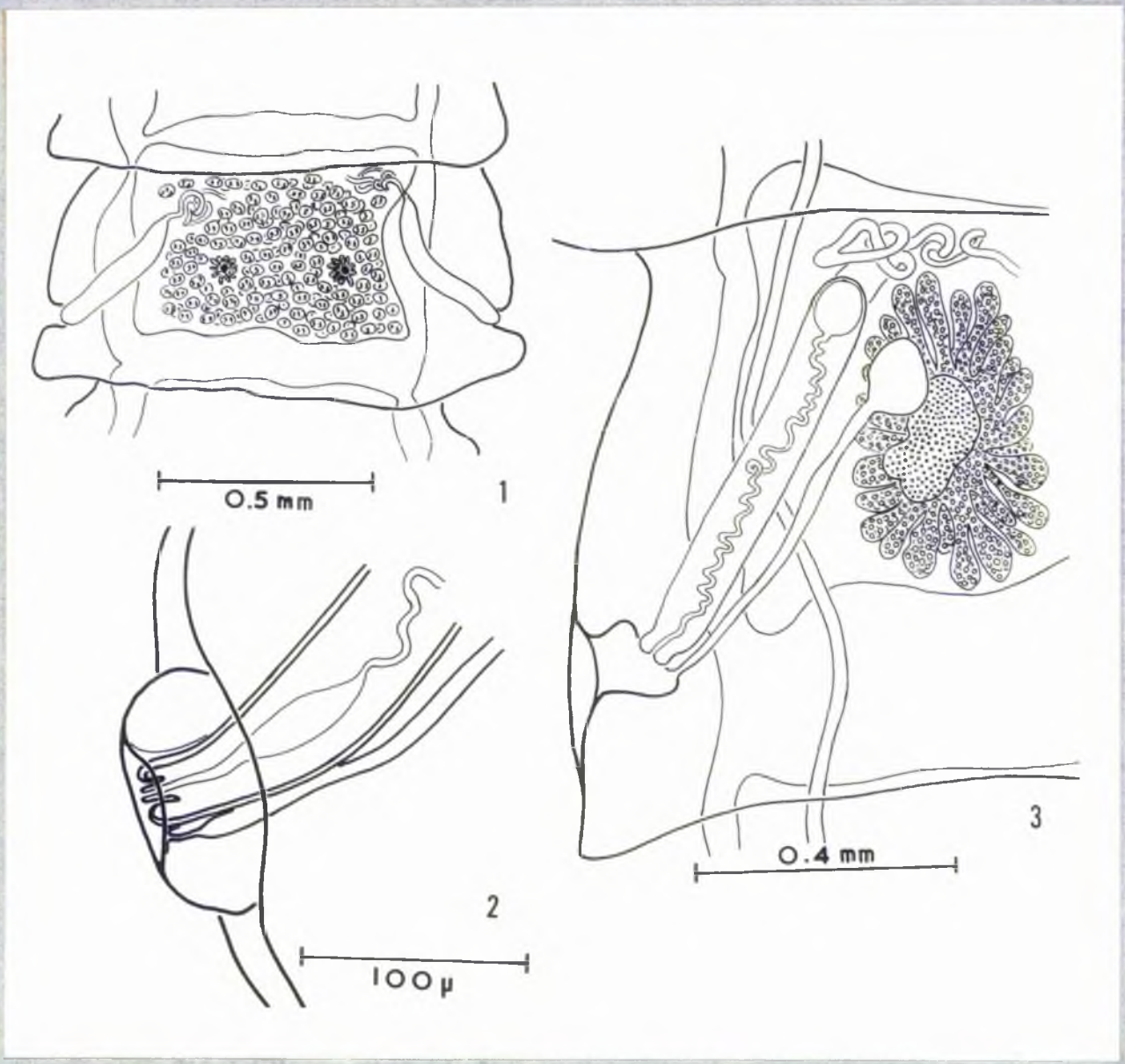
Only fragments of what appears to be one, incomplete worm are present and these total about 80 mm in length. The maximum breadth is 2 mm. The proglottides are all broader than long with a tendency, in the more gravid proglottides, to become square.

The scolex is missing.

The testes are numerous (Fig. 1) and develop before the ovaries. Over 150 testes were seen in one proglottis, but they are difficult to count accurately owing to the displacement of the genitalia by the unnaturally swollen excretory vessels. In some proglottides, the testes attain a maximum diameter of about 70μ but are generally smaller averaging about 55μ in diameter. The cirrus sac measures 400-600μ in length but may be longer as, in many instances, there are pronounced twists which tend to foreshorten it. The diameter of the cirrus sac remains fairly constant at 40-55μ and in some proglottides the cirrus can be seen protruding as a short nipple-like projection from the genital atrium.

* Host name and number according to collection records.

The deeply lobed ovaries are 380-520μ by 200-240μ and are fan-shaped (Fig. 2). The vitelline glands, which measure 150-170μ by 110-125μ, tend to be surrounded by the ovarian lobes (Fig. 3).



Figs 1-3. Paronia bocki Schmelz, 1941. Early proglottis showing distribution of testes (Fig. 1), opening of cirrus sac (Fig. 2), and part of a later proglottis showing one of the two ovaries and the associated vitelline gland (Fig. 3).

The uterus breaks down into uterine capsules each of which contains but a single egg. Although initially the two uteri are quite separate, the capsules eventually fill the whole proglottis. The outer membrane of the egg measures 50-60μ by 38-48μ and the inner membrane measures 28-34μ in diameter. The hooks of the oncospheres were not sufficiently clearly seen to be measured.

The excretory vessels appear to be unnaturally swollen and have the effect of crowding the genitalia into isolated regions in most proglottides. The transverse excretory vessel which joins the two ventral excretory vessels posteriorly in each proglottis, is particularly prominent and swollen in fully mature and gravid proglottides.

DISCUSSION:

Schmelz (1941) differentiates his species from Paronia carrinoi Diamare, 1900 on the formation of the uterus in gravid proglottides. In P. bocki, the two uteri eventually join to form a continuous field of uterine capsules whereas in P. carrinoi both uteri remain separate. This feature together with the difference in the size of the cirrus sac also serve to differentiate P. bocki from P. pycnonoti Yamaguti, 1935. Although the number of

testes in the present material may be fewer than the number described by Schmelz and although there is a slight discrepancy in the sizes of the ovaries (380-520μ by 200-240μ in the present material and 700 by 290μ in Schmelz's material) in view of the close agreement of other characters, there seems little doubt that the present material should be ascribed to P. bocki Schmelz, 1941. Further differences between the known species of Paronia can be seen readily in Table 1.

P. carrinoi is listed by Yamaguti (1959) as P. carrinii and is included as a synonym of P. trichoglossi (Linstow, 1888). As indicated by Spasski (1951), Linstow, in his original description, mentions only the total length and breadth of the worms, the sizes of different proglottides, and the size of the eggs and oncospheres. Furthermore, Linstow indicates that "The specimens possibly belong to Taenia leptosoma, Diesing, found in various parrots", and this worm, T. leptosoma, is now considered as belonging to the genus Raillietina. It would appear then that the grounds for including Diamare's species as a synonym of such an inadequately described worm, are not really sufficient and it is here proposed that the specific name carrinoi be retained and that it should not become a synonym of P. (?) trichoglossi.

Species:	Strobila length in mm	Strobila max. breadth in mm	Scolex diameter in microns	Cirrus Sac length in microns	Testes No.	Testes Diameter in microns	Gravid Uterus	Egg diameter in microns	Host	Locality
P. ambigua (Fuhrmann, 1902)	60-80	1.5	-	120	100	60	single	30	Amazona amazonica RHAMPHASTIFORMES	Brazil
P. beauforti (Janicki, 1906)	18	3	-	600	360	-	single	-	Cyclopsittacus diophthalmus PSITTACIFORMES	New Guinea
P. biuterina Burt, 1939	55	2.25	265	215-272	65-75	38	double	27-30	Coryllinus beryllinus PSITTACIFORMES	Ceylon
P. bocki Schmelz, 1941	70-75	5	800	700	200-220	77	single	40	Megalaema virens Cyanops ramsayi PICIFORMES	Siam
P. calcaruterina Burt, 1939	126	2.1	690	380-420	102-120	85	double	31-32.5	Molpastes haemorrhous PASSERIFORMES	Ceylon
P. carrinoi Diamare, 1900	70-120	3-5	530	450-700	140-150	45 x 10	double	30	Trichoglossus novaehollandiae; T. nigrigularis; Cyclopsittacus suavissimus; Lorius erythrothorax PSITTACIFORMES	Australia; New Guinea
P. columbae (Fuhrmann, 1902)	-	1	-	90	200	-	single	30	Columba sp. (?) Ptilonopus sp. (?) COLUMBIFORMES	Sumatra; Bengal
P. coryllidis Burt, 1939	70-75	1.2	305-315	325	70-80	68	single	21-24	Coryllis beryllinus PSITTACIFORMES	Ceylon
P. pycnonoti Yamaguti, 1935	40-55	2.5-3.2	480-580	250-400	80-125	-	double	42-48	Pycnonotus sinensis PASSERIFORMES	Formosa
Taenia trichoglossi von Linstow, 1888	over 80	2.1	missing	-	-	-	-	36 (outer) 26 (inner)	Trichoglossus swainsoni PSITTACIFORMES	Australia
P. variabilis (Fuhrmann, 1904)	70	2.5	450	270	100	40	single	43	Rhamphastos culminatus; R. dicolorus; R. toco; R. erythrorhynchus. PSITTACIFORMES	South America
P. zavattari Fuhrmann and Baer, 1943	-	1.4-3.3	-	300	-	-	double	36-40	Colius striatus COLIIFORMES	Ethiopia
Borneo material	over 80	2	-	400-600	over 150	55-70	single	50-60 x 38-48	Megalaema chrysopogon PASSERIFORMES	Borneo

Table I

Paronia species to show various differences and similarities to the present material from Borneo.

Raillietina (Raillietina) echinobothrida (Mégnin, 1881)

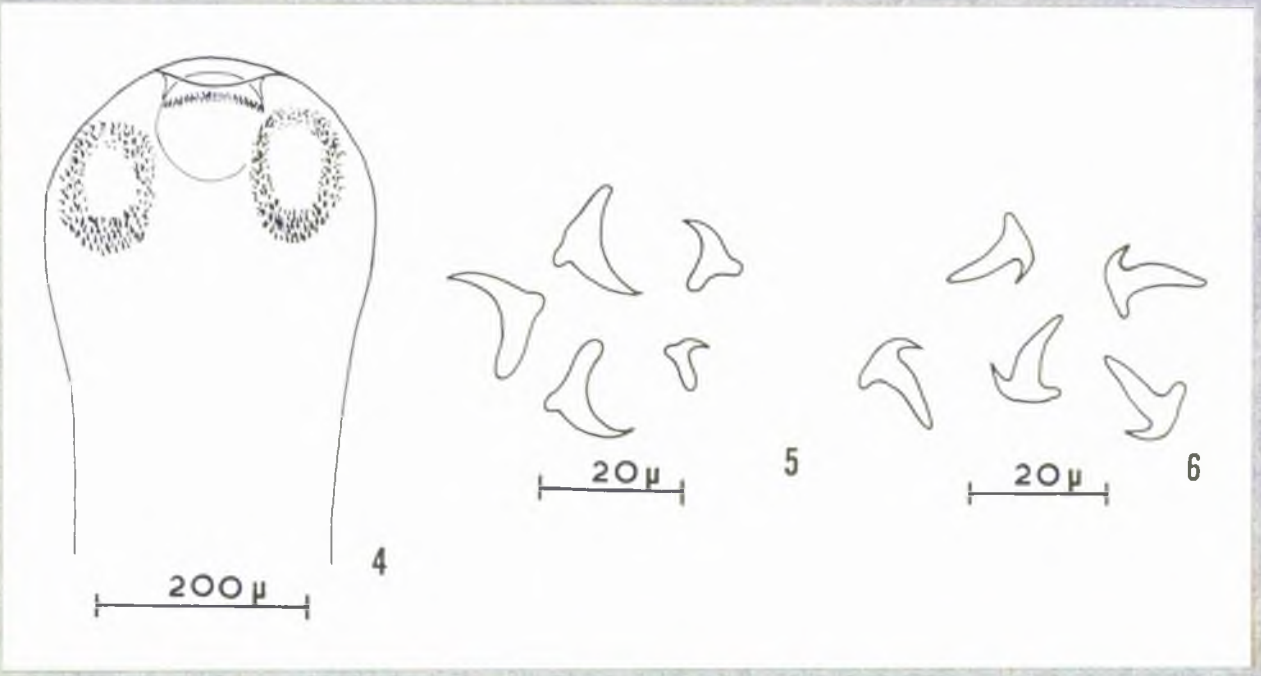
Syn.: Taenia bothrioplites Piana, 1881
Davainea paraechinobothrida Magalhães, 1898
Davainea volzi Fuhrmann, 1905
Davainea penetrans Baczynska, 1914
Raillietina grobbeni Böhm, 1925
Raillietina pseudoechinobothrida Meggitt, 1926

Host: Domestic fowl (Gallus gallus (L.) dom.) 8696

The longest specimen is 105 mm long with a maximum breadth of about 3 mm. The proglottides are all much broader than long, the ratio of breadth to length tending to increase from immature to mature proglottides and tending to decrease from mature to gravid proglottides. The genital apertures are unilateral and are situated laterally and slightly posteriorly to the middle of each proglottis. The genital ducts pass between the dorsal and ventral excretory vessels.

The size of the scolex (Fig. 4) shows considerable variation measuring 170-265μ long by 240-330μ broad. The four suckers are circular to oval in outline and measure 90-155μ by 52-90μ. They are profusely armed with spines (Fig. 5) which are 9-17μ long. The rostellum, when everted, is roughly spherical with a diameter of about 100μ. It is armed with a double circlet of about 200 hooks (Fig. 6) which are 12-14μ long.

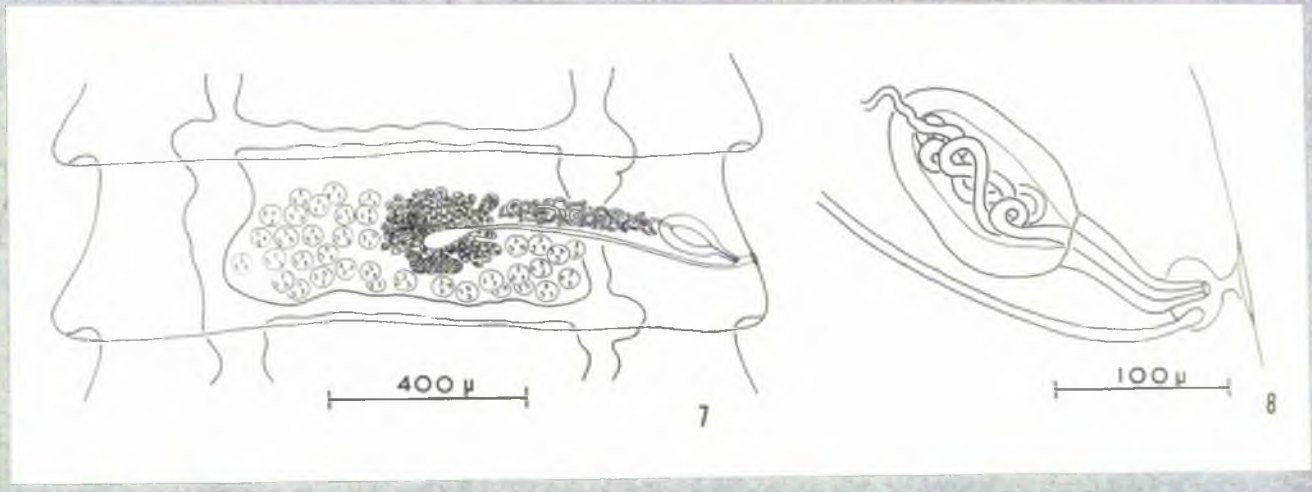
There are 20-45 testes which lie in two lateral fields (Fig. 7): those aporally comprise over half the total number. In many proglottides there are one, two or three testes which lie posteriorly or dorsally to the vitelline gland and which connect the two lateral fields.



Figs 4-6. Raillietina (Raillietina) echinobothrida (Megnin, 1881). Scolex (Fig. 4), sucker spines (Fig. 5), and rostellar hooks (Fig. 6).

The cirrus sac (Fig. 8) measures 120-145μ by 74-83μ and opens into the genital atrium in the posterior half of each proglottis. It is bulbous in shape and strongly muscled. The vas deferens is much coiled and lies in the anterior portion of each proglottis, in front of the ovary, and in fully mature proglottides it becomes greatly distended with sperm.

The ovary which is fan-shaped and digitate lies in the middle of each proglottis. Its total breadth varies from 380μ to 405μ. The vitelline gland lying immediately behind the ovary, is compact and irregularly ovoid measuring 120-140μ by 70-80μ. Between the ovary and the vitelline gland lies the shell gland which is dorsal to the receptaculum seminis. In only one proglottis could the receptaculum seminis be measured accurately and there it measured 49μ long by 38μ in diameter. The vagina, in fully mature and early gravid proglottides, appears swollen with sperm in the region of the ovary.



Figs 7 and 8. Raillietina (Raillietina) echinobothrida (Mégnin, 1881). Mature proglottis (Fig. 7) and cirrus sac (Fig. 8).

The uterus is more or less sac-shaped initially but later extends laterally beyond the excretory vessels and breaks down to form uterine capsules which measure 110-170μ in diameter. In over 85% of the capsules there

are four or five eggs, but occasionally two, three or six eggs may be present in a capsule. The eggs are slightly ovoid and measure 42-52μ by 32-42μ. The hooks of the oncosphere are 6-7μ long.

DISCUSSION:

Although the group echinobothrida (Mégnin, 1881) sensu lato shows considerable variation among its component species or subspecies, particularly with reference to the arrangement of genital apertures, number of testes and number of eggs per capsule (see Table II), these differences do not appear to be either sufficiently great nor, and perhaps of more importance, sufficiently constant to justify the separation of any distinct species other than echinobothrida.

Ransom (1904) discusses fully the problems of synonymity of echinobothrida up to that time and more recently Lang (1929) regards the following as synonyms of echinobothrida (Mégnin, 1881): Davainea volzi Fuhrmann, 1905; Davainea penetrans Baczynska, 1914; Raillietina (R.) grobbeni Böhm, 1925; and Raillietina pseudoechinobothrida Meggitt, 1926. As can be seen from Table II there is a wide range of overlap in most characters even as to the arrangement of the genital apertures. Mégnin (1881),

Species:	echino-bothrids	botria-pitis	paraschino-bothrids	echino-bothrids	volsi	penetrans	tenetrans	echino-bothrids	echino-bothrids var. bothrio-pitis	grobbeni	pseudo-echino-bothrids	echino-bothrids	echino-bothrids	echino-bothrids	Borneo material
Described by:	Meggitt 1931	Plana 1882	Magalhaes 1898	Ransom 1904	Fuhrmann 1905	Baczynska 1914	Skrjabin 1914	Lopez-Neyra 1920	Lopez-Neyra 1920	Bohm 1925	Meggitt 1926	Lang 1927	Sawada 1955	Yamaguti 1956	
Strobila (length x max. breadth in mm)	50-100 x 4	200 x 3		250 x 4	40-60 x 2	30-40 x 1-5	180 x 3	150 x 4	230 x 4	170-440 x 4.1	80-90 x 1.8	35-200 x 3	120-250 x 4	60-160 x 2.4	105 x 3
Scolex (diameter in μ)	-	350		250-450	450	352	374	250-450	250-450	344	-	286-343	250-550	250-400	170-255
Mostellum (diameter in μ)	-	140 (from drawing)	Differs from echinobothrids of Meggitt only in the fact that it has unilateral genital apertures.	100-150	88	104	-	88-150	88-150	96	-	96-107	100-140	100-130	100
Rostellar hooks (number)	100	200		200	240	240	240-300	200-240	200-240	200	200	120-140	200	-	200
Rostellar hooks (length) in μ	8	10-15 (from drawing)		10-13	10	13	13	10 & 13	10 & 13	10 & 13	8-12	10 & 13	10-13	10 & 12	12-14
Suckers (diameter in μ)	large	120-130 (from drawing)		90-200	180	169	-	90-200	90-200	125	-	120-140	130-200	210	52-115
Sucker spines (number of rows)	7	7-8		8-10	Ant.=12-14 Post.=4-6	14-15	-	10-15	10-15	-	-	8-12	10-13	9-14	Several
Sucker spines (length in μ)	-	6-19 (from drawing)		6-15	8-12	-	-	8-15	8-15	7-17	-	5-15	4-20	up to 12	9-17
Testes (number)	-	-		20-30	30	15-20	30-35	20-?	20-35	24-32	30-50	25-45	25-45	38-48	20-45
Testes (diameter in μ)	-	-		-	30-36	41.6	-	39-43	39-43	54	-	38-67	-	24-60	35-60
Cirrus sac (length in μ)	-	-		130-180	200-230	163	163	130-200	130-190	182-187	-	150-200	150-165	120-190	120-145
Eggs (number per capsule)	6-7	-		8-12	8-12	-	-	8-12	8-12	up to 6	3-4	4-10	3-8	5-9	2-6
Eggs (diameter in μ)	90	-		25-50	20-25	-	-	25-40	25-40	24-37	-	34-48	73-77	27-42	32-52
Oncospheres (diameter in μ)	-	-		-	13	10.4	-	10-14	10-14	10-15	-	10-18	24-26	10-15	12-18
Genital apertures (arrangement)	Irregularly alternating	Unilateral		Irregularly alternating	Unilateral	Unilateral	Unilateral	Irregularly alternating	Unilateral	Unilateral	Irregularly alternating	Unilateral	Unilateral or Irregularly alternating	-	Unilateral

Table II

Species presently included in Baillietina (Baillietina) echinobothrids sensu lato to show the wide range in morphological characters.

Ransom (1904), Lopez-Neyra (1920) and Meggitt (1926) all describe material with irregularly alternating genital apertures. Ransom, however, further states that they are sometimes almost entirely unilateral. Lopez-Neyra (1920), discussing the synonymity of those species closely related to echinobothrida, is of the opinion that there are two distinct varieties: the one with irregularly alternating genital apertures which contains Mégnin's original species; and the other with unilateral genital apertures which is the variety bothrioplitis and which includes Davainea paraechinobothrida Magalhães, 1898, D. volzi Fuhrmann, 1905 and D. penetrans Baczynska, 1914. Lopez-Neyra, however, figures part of a strobila of echinobothrida var. bothrioplitis in which the genital apertures exhibit alternation. Although Meggitt (1926), in his descriptions of echinobothrida (Mégnin, 1881) and of pseudoechinobothrida, states that the genital apertures are irregularly alternate, he modified this in a letter written to D.R.R. Burt and dated August 27, 1936, when he said: "I have looked over my slides of R. echinobothrida and R. pseudoechinobothrida, and I find that the genital aperture is invariably unilateral. I think that the mis-understanding arises from the fact that an occasional genital pore is on the wrong side,

but this is so seldom as not to count." It would thus appear that the variation in the arrangement of the genital apertures is of little real significance in this species and that what was true of Meggitt's material was probably true of the other three instances. Accordingly, as the apertures which appear on the "wrong" side seem to be so few these probably constitute nothing more than exceptions to the general pattern of unilateral arrangement.

While discussing the problem of synonymity of echinobothrida with Professor J.G. Baer, he made the interesting observation that those species within the group echinobothrida sensu lato show a tendency to fall naturally into two separate, smaller groups: those from Europe; and those from Asia. In the case of those species recorded from Europe there appear to be fewer testes and more eggs per capsule than in those species recorded from Asia. There is, nevertheless, some degree of overlap between these two conditions and it probably would be unwise to do more at the present time than record this observation of differences, due apparently to geographical distribution.

It is clear that the whole question of synonymity of echinobothrida sensu lato will have to be gone into

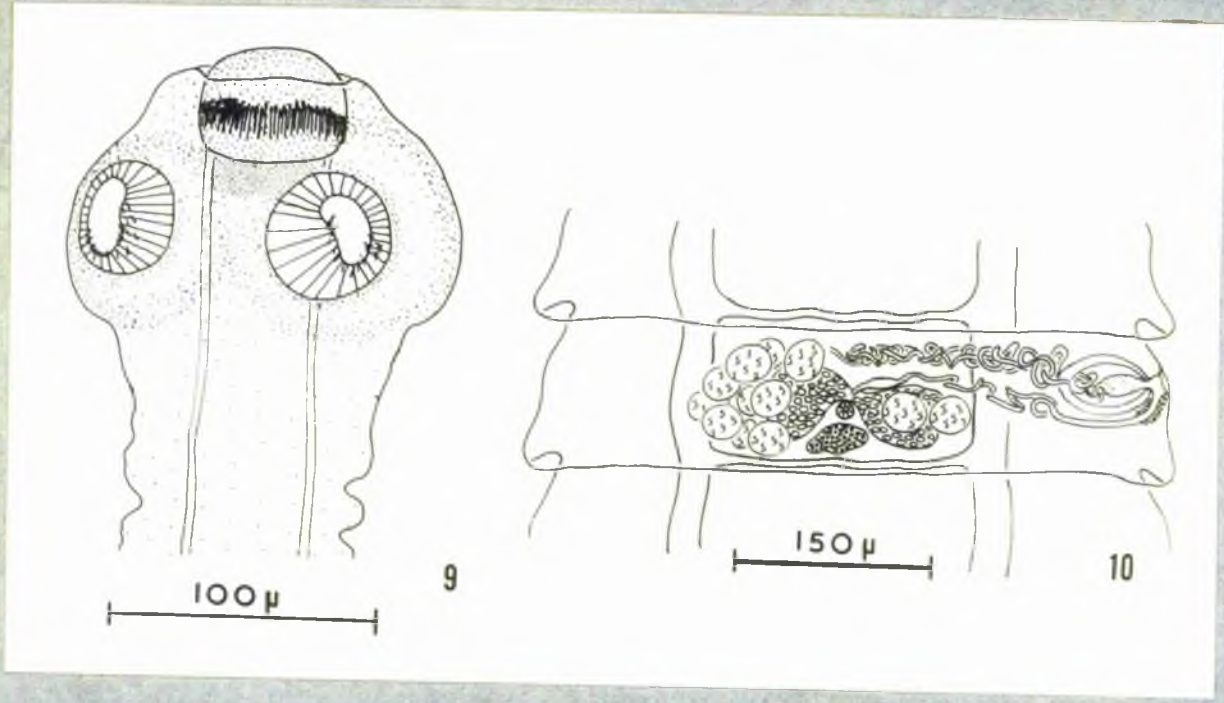
more fully and with more material from Asia particularly. Work is at present in hand on a large collection of cestodes from Ceylon, made by D.R.R. Burt, and it is hoped that the result of this investigation may throw more light on the above problems.

Raillietina (Raillietina) johri Ortlepp, 1938

Syn.: Raillietina (Raillietina) polychalix of Johri, 1934, nec Kotlan, 1921.

Host: Treron vernans 8963; 9044; 9433; 9545.

The mature worms measure 50-70 mm long by 0.6-1.0 mm in maximum breadth. The proglottides are all broader than long, the breadth varying from two to five times the length depending upon the degree of contraction of the strobila. The genital apertures are unilateral and open in the anterior half of the margin of each proglottis. The genital ducts pass between the longitudinal excretory vessels.



Figs 9 and 10. Raillietina (R.) johri Ortlepp, 1938. Scolex (Fig. 9) and mature proglottis (Fig. 10).

The scolex (Fig. 9) measures 90-130μ by 60-150μ and bears four armed suckers. The diameter of the suckers is 40-85μ and the spines, which are up to 10μ long, are easily lost and were not seen in all specimens. The rostellum, 60-68μ in diameter, bears a double crown of hooks, those in the anterior row measuring 15μ long and those in the posterior row measuring 12μ long.

There are 6-12 testes usually divided into two groups which lie on either side of the female genitalia (Fig. 10). The poral group contains one to three testes while the majority lie aporally. The testes are ovoid to spherical and measure 50-70μ by 36-60μ. The cirrus sac, 85-115μ long by 40-60μ in diameter, is roughly flask-shaped and has a thick muscular wall. In a few proglottides the profusely armed cirrus could be seen as a small bulbous projection from the genital atrium. There is an internal seminal vesicle with a diameter of 15-30μ. The vas deferens is much coiled and lies parallel to the anterior margin of each proglottis.

The bilobed ovary lies in the centre of the proglottis and measures 115-135μ across both lobes. The vitelline gland, situated posteriorly to the isthmus of the ovary, is compact and measures 45-75μ by 30-55μ.

The shell gland, 20-25μ in diameter, lies more or less centrally over the isthmus of the ovary occasionally being slightly displaced so that it lies partly over one of the lobes of the ovary. The vagina expands before reaching the centre of the proglottis to form a receptaculum seminis, 25-45μ long by 15-25μ in diameter. The opening of the vagina is posterior to the opening of the cirrus sac.

The uterus breaks down to form 18-30 capsules per proglottis and occasionally more, the size of the capsules varying from 50-80μ in long diameter by 40-65μ in short diameter. In some few capsules, which contained more than the normal number of eggs, the long diameter reached as much as 100μ or more. There are 8-12 eggs per capsule usually, while some capsules contained as few as 6 and others as many as 16 eggs. The eggs measure 35-40μ by 27-33μ and the contained oncospheres are about 15μ in diameter.

DISCUSSION:

Raillietina (Raillietina) polychalix Kotlan, 1921 was described by Johri (1934) as coming both from Psittacula krameri manillensis and from Columba livia domestica although those worms from Columba differed quite markedly

from those found in Psittacula. According to Johri, however, these differences were not sufficiently great to warrant separation of the worms and the erection of a new species and accordingly the worms from both hosts were identified as polychalix. Ortlepp (1938), however, feels that the differences between those worms from Columba and those from Psittacula are too great to allow the inclusion of both groups of worms in the species polychalix and erects a new species, Raillietina (Raillietina) johri, to contain those worms which were found in Columba livia domestica. The two differences that Ortlepp considers to be most significant are the different sizes of the cirrus sac and the different number of rostellar hooks (See Table III).

Perhaps it should also be pointed out that the worms described by Johri that came from Psittacula show even less similarity to Kotlan's species polychalix than did the worms from Columba and accordingly it would appear that neither of the worms which Johri described is in fact polychalix Kotlan. Proper identification of the worms from Psittacula will have to await a full re-examination of the material and comparison with known species.

Host	Number of rostellar hooks	Length of cirrus sac
Columba	324	125-130μ
Psittacula	190	61μ

Table III

Raillietina (Raillietina) polychalix Kotlan, 1921 as described by Johri (1934).

The present material agrees well with the few characters that are given for Raillietina (Raillietina) johri and also seems to differ in one or more characters from all other species of Raillietina from birds where the size of rostellar hooks is within the same range of 12-15μ and where the number of testes also falls within the same range of 6-12 testes per proglottis (See Table IV). As can be seen, the only species with which the present material does not differ significantly, apart from johri, is Raillietina (R.) circumcincta (Krabbe, 1869) but this worm is very poorly described and furthermore comes from a well separated order of birds, the Ciconniiformes.

According to the label in one of the tubes containing worms of the present species the host is Tringa glareola, a charadriiform bird, but as there does not appear to be any substantiated record of a Raillietina from any member of the Charadriiformes (see discussion following description of Kowalewskiella susanae n. sp.), it is not unlikely that there may have been a mix-up in the labels. All measurements of the present material from Tringa glareola are recorded separately, as follows, to facilitate comparison in the event of there being any further recorded Raillietina from a Charadriiform bird.

Strobila - 41 by 1.15 mm; scolex - 165 by 210μ; rostellum - 100μ diam.; rostellar hooks - 200-250 hooks, in double circle, about 12μ long (size measured from whole mount); suckers - armed, 65-70μ in diameter; genital apertures - unilateral; testes - 6-11, 37-52μ in diameter, on both sides of the female genitalia; cirrus sac - 95-130μ by 50-75μ; internal seminal vesicle present; ovary-bilobed; vitelline gland - median, posterior to ovary, ovoid; receptaculum seminis - 59μ by 45μ; egg capsules - not extending beyond longitudinal excretory vessels, containing about seven eggs per capsule.

Species:	*circumcincta* Krabbe, 1869	*micracantha* Fuhrmann, 1909	*micracantha* Fuhrmann, 1909	*provincialis* Linstow, 1909	*spiralis* Baczynska, 1914	*bycanistis* Baylis, 1919	*polychalix* Kotlan, 1920	*polychalix* Kotlan, 1920	*johri* Ortlepp, 1938	Borneo material
Description taken from:	Krabbe 1869	Fuhrmann 1909	Lopez-Neyra 1931	Linstow 1909	Baczynska 1914	Baylis 1919	Kotlan 1920	Johri 1934	Johri 1934	
Strobila (length x max. breadth in mm)	120 x 2	100 x 0.8	180 x 1.2	60 x 1.58	30-40 x 1.28	140 x 2	55 x 1.7	103	273 x 0.75	50-70 x 1
Scolex (diameter in μ)	-	180	180-200	280	224	270	320	-	260	90-130
Rostellum (diameter in μ)	-	-	117-135	-	150	150	148	-	-	60-68
Rostellar hooks (number)	300	200	150	500	300	-	240-250	190	324	
Rostellar hooks (length in μ)	11-12	13-14	12-147	14.3	15.6	15	13	13.5 & 19	11 & 14	12 & 15
Suckers (diameter in μ)	-	-	50-65 x 40-50	130	52	88	-	-	-	40-85
Sucker spines (length in μ)	-	-	9-10	-	-	13	-	-	6-7	10
Testes (number)	-	-	14-18	10-12	6-7 (by implication)	12-14	10-12	9-11	8-9	5-12
Testes (diameter in μ)	-	-	50 x 45	57-68	39	75	40	-	-	50-70 x 36-60
Cirrus sac (length x diameter in μ)	-	-	110-140 x 40-60	-	101	200 x 62	120	61	125-130	85-115 x 40-60
Eggs (number per capsule)	-	-	4-7	several	4-6	4-5	2-5	-	6	8-12 (5-16)
Eggs (diameter in μ)	-	-	38-42 x 35-40	52	-	-	-	-	-	35-40 x 27-33
Oncospheres (diameter in μ)	-	-	14-15	18	-	15	-	-	-	15
Avian host (order)	Ciconiiformes	Columbiformes	Columbiformes	Galliformes	Columbiformes	Coraciiformes	Psittaciformes	Psittaciformes	Columbiformes	Columbiformes

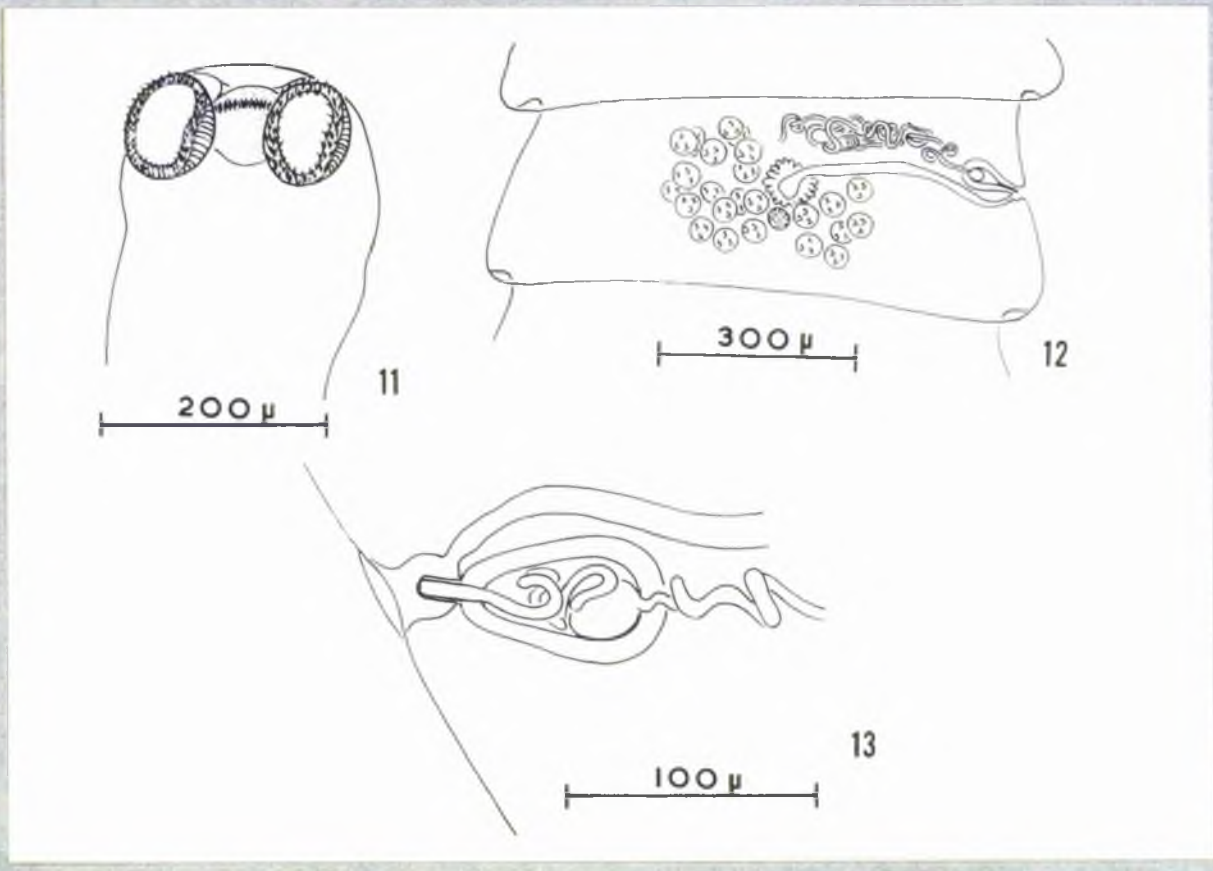
Table IV

Raillietina (*Raillietina*) species from birds with rostellar hooks in the range 12-15μ long and with 6-12 testes.

Raillietina (Raillietina) parviuncinata Meggitt et Saw, 1924

Host: Domestic fowl (Gallus gallus (L.) dom.) 8696

The mature worm measures 35 mm long by 0.9 mm in maximum breadth. The proglottides are broader than long, but only immature and early mature ones are present. The genital apertures are unilateral and open in the anterior half of the margin of each proglottis.



Figs 11-13. Raillietina (R.) parviuncinata Meggitt et Saw, 1924. Scolex (Fig. 11), mature proglottis (Fig. 12), and cirrus sac (Fig. 13).

The scolex (Fig. 11) measures 170µ long by 240µ in diameter and bears four heavily armed suckers. The

suckers are oval measuring 92-100 x 52-66μ and the sucker spines, while being difficult to measure accurately, appear to reach up to 12μ long. The rostellum is not evaginated and bears a complete double row of about 200 hooks which are 8-10μ long.

In the early mature proglottides present, the testes number 20 to 30 and are 38-46 x 34-43μ. The cirrus sac was not clearly seen but appears to be about 70-80μ long by about 40-50μ in diameter.

DISCUSSION:

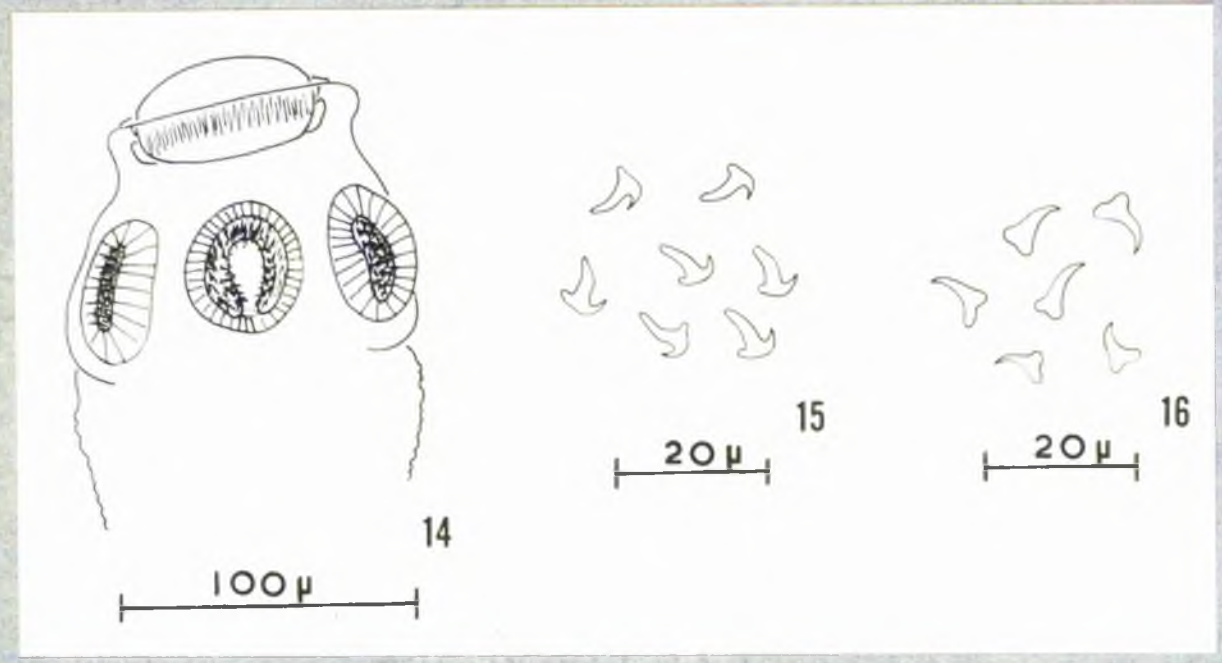
Although there are several discrepancies between the present material and those described by Meggitt and Po Saw (1924), it is apparent that in their description there are several typographical errors. The maximum breadth of the worm, for instance, is quoted as being 0.2 mm and yet in the text figure on page 325 a mature proglottis is drawn which, according to the scale given, measures over 1.0 mm in breadth. The cirrus sac in their description is described as being 0.58 to 0.84 mm in length, whereas it is again clear from the drawing on page 325 that the length should be 0.058 to 0.084 mm.

In view of the close agreement between the length of rostellar hooks (7-9μ - Meggitt and Po Saw; 8-10μ - present material); the number of testes (24-39 - Meggitt and Po Saw; 20-30 - present material); and the length of the cirrus sac (58-84μ - Meggitt and Po Saw; 70-80μ - present material) the present material is tentatively identified as Raillietina parviuncinata. This identification should remain tentative owing to the fact that parviuncinata was recorded initially from an anseriform bird whereas the present material comes from a galliform bird. So far as can be ascertained, however, the present worms do not resemble any known species from a galliform bird well enough to warrant identification with them.

Raillietina (Raillietina) sequens Tubangui et Masiluñgan, 1937

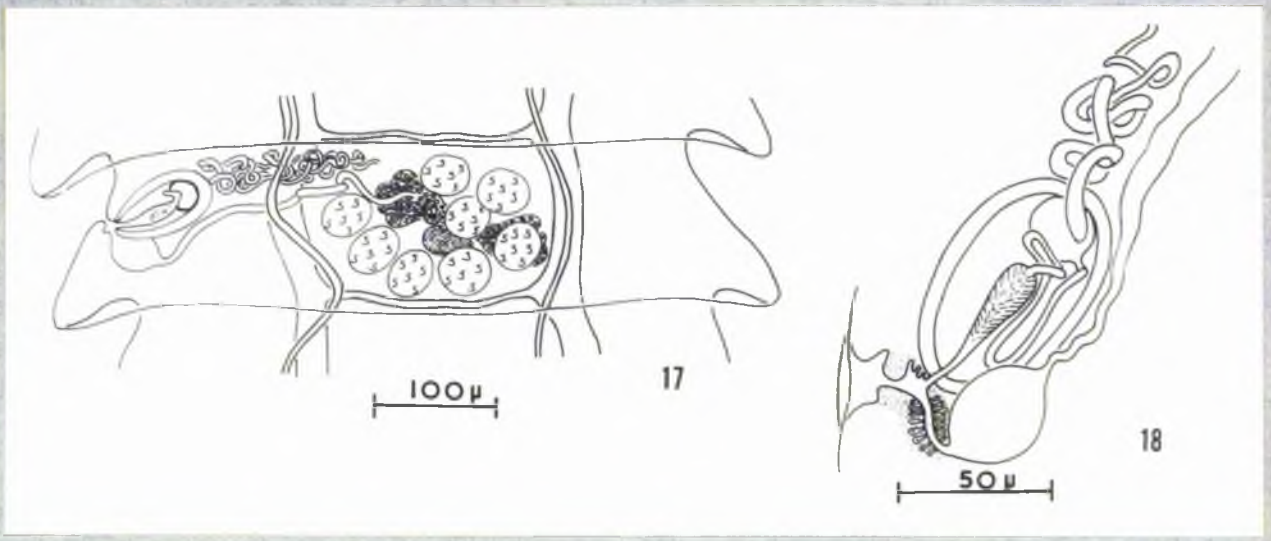
Hosts: Domestic pigeon (Columba livia Bonn. dom.) 9019.
Streptopelia chinensis 9409, 9151.
Aegithina tiphia 9047.

The largest worm measures 100 mm in length and the maximum breadth is 1.5 mm. The proglottides are all broader than long with the ratio of breadth to length generally increasing towards the posterior end of the worm. The genital apertures are unilateral and the genital ducts pass between the excretory vessels.



Figs 14-16. Raillietina (R.) sequens Tubangui et Masiluñgan, 1937. Scolex (Fig. 14), rostellar hooks (Fig. 15), and sucker spines (Fig. 16).

The scolex (Fig. 14) varies in diameter from 80 to 122μ and bears a rostellum which measures 45-90μ in diameter by 30-53μ long. The rostellar hooks (Fig. 15) are arranged in two separate rows: those of the anterior row being slightly larger, measuring 7.5-8μ in length while those of the posterior row measure only 6-7μ in length. The four suckers measure 30-51μ by 20-45μ and are armed with spines (Fig. 16) which are 2-10μ long.



Figs 17 and 18. Raillietina (R.) sequens Tubangui et Masilungan, 1937. Mature proglottis (dorsal view) (Fig. 17) and cirrus sac (ventral view) (Fig. 18).

There are 6-10 testes (Fig. 17) one to three usually lying porally, which measure 45-60μ by 40-55μ. The cirrus sac (Fig. 18) is 80-115μ long by 40-60μ in

diameter and contains a slightly coiled cirrus, which is armed with hair-like, cuticular spines, and an internal seminal vesicle of 35-40μ by about 30μ. The vas deferens becomes greatly swollen with sperm and highly twisted.

The ovary is bilobed with each of the two lobes tending to subdivide further into smaller lobules. It is situated medially and ventrally being contained within the confines of the ventral excretory vessels. The vitelline gland, lying immediately posteriorly to the ovary, is irregularly ovoid and measures 30-40μ in diameter. Immediately in front of the vitelline gland but posterior to the ovary, is the shell gland of 20-25μ in diameter. The receptaculum seminis is just posterior to the cirrus sac and tends, in many cases, to lie slightly ventrally to the cirrus sac. It is highly variable in size measuring up to 50μ by 25μ.

The uterus, which arises immediately dorsally to the shell gland, is initially a sac-like structure but eventually occupies the whole of the medulla before breaking down into uterine capsules. The number of capsules per proglottis is variable but generally falls between 50 and 70, each capsule measuring 50-100μ by 35-55μ. There are 2-8 oncospheres per capsule and these

measure 25-40μ by 15-35μ. The hooks of the oncospheres are small ranging from 5.5μ to about 7μ in length.

DISCUSSION:

As can be seen in Table V there are several worms which have only a few testes and which also possess small rostellar hooks. In many instances the only difference between separate species is that one species may have one or two testes more, or fewer, than another. This hardly seems to be a justifiable criterion for the erection of new species as it is abundantly clear in the present material that the range in number of testes is fairly wide. However, it should be noted that this range of 6-10 testes was not seen in any single worm but represents the total range in all the worms which otherwise were more or less identical from the different hosts mentioned. Thus, some individual worms showed a range of 6-7 testes; others a range of 6-8; others a range of 8-10 and so on. While this observation could be interpreted as indicating that there were two or more separate species present, in view of the extremely close similarity of other features and the fact that there was no other constant difference manifest between worms showing differences in number of testes, it is here proposed that the range of 6-10 testes represents an intraspecific

Species:	cryptacantha Fuhr., 1909	paucitesticulata Fuhr., 1909	cacatuina Johnst., 1911-13	calyptomenae Baylis, 1925	flabralis Meggitt, 1927	flaminiata Meggitt, 1931	fragilis Meggitt, 1931	fulvia Meggitt, 1933	sequens Tub. & Mas., 1937	Borneo material
Description taken from:	Fuhrmann (1909)	Fuhrmann (1909)	Lopez-Neyra (1931)	Baylis (1926)	Meggitt (1927)	Meggitt (1931)	Meggitt (1931)	Meggitt (1933)	Tubangui & Masilungen (1937)	
Strobila (length x max. breadth in mm)	120 x 1.5	100 x 0.6	50 x 0.53	60-100 x 1.15	350 x 1	50 x 0.6	190 x 0.9	? x 6.0	170 x 1.1	100 x 1.5
Scolex (diameter in μ)	140	100	114	170-250	216	720	150	110-120	100	80-122
Rostellum (diameter in μ)	59	44	-	100-125	80	-	73	35-40	60	45-90
Rostellar hooks (number)	170	120	-	Very	[illegible]	-	-	-	180	-
Rostellar hooks (length in μ)	7.2	9-10	Ca. 6	8	6	9	6-9	-	7.6-8	6-8
Suckers (diameter)	36	27	45	55-80	-	-	-	-	40	30-51 x 20-45
Sucker spines (number of rows)	-	-	Several	-	-	-	several	several	-	several
Sucker spines (length in μ)	-	-	7.5	minute	-	-	-	-	-	2-10
Testes (number)	8-12	6-7	4-5	5	4-5	5-9	8-9	8-10	5-6	6-10
Testes (diameter in μ)	68	-	20	-	-	-	-	-	55-70	40-60
Cirrus sac (length x diameter in μ)	-	120-140	65-100 x 20-42	160 x 55	up to 120	110-130 x 40-60	120 x 60	92-106 x 54-64	100-120 x 40-60	80-115 x 40-60
Eggs (number per capsule)	-	6-8	12	8	10	2-6	4-6	1	2-8	2-8
Eggs (diameter in μ)	-	-	44 x 19	-	-	-	-	-	34.5-46	-
Oncospheres (diameter in μ)	-	-	-	-	-	-	-	35-40	19-23	25-40 x 15-35
Genital apertures (arrangement)	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral
Avian host (order)	Columbiformes	Columbiformes	Psittaciformes	Passeriformes	Coraciformes	Columbiformes	Columbiformes	Pterocletiformes	Columbiformes	Columbiformes

Table V

Raillietina species possessing rostellar hooks under 10u long and with 5-10 testes.

variation in the species R. sequens. Furthermore a re-examination of the species listed in Table V, and also many other species in the genus Raillietina, may very well show that the intraspecific variation is so great that several species which at present are considered as distinct should in fact be united into a single species. In view of the fact that it has not been possible, as yet, to see sufficient type material, redescriptions from the suggested re-examination will not be presented at this time.

Except in the number of testes, as has just been discussed, the present material appears to agree in all respects with worms described by Tubangui and Masiluñgan (1937) as Raillietina (R.) sequens and is, accordingly, here identified as that species.

Raillietina (Raillietina) allomyodes Kotlan, 1921

Host: Treron vernans 8951

One mature, but non-gravid, worm was present. It measures 15 mm long and has a maximum breadth of 0.8 mm. The worm is highly contracted and accordingly the shape of the proglottides, which ranges from 24 times broader than long in immature proglottides to 11 times broader than long in the last mature proglottides, is of little significance. The genital apertures are unilateral.

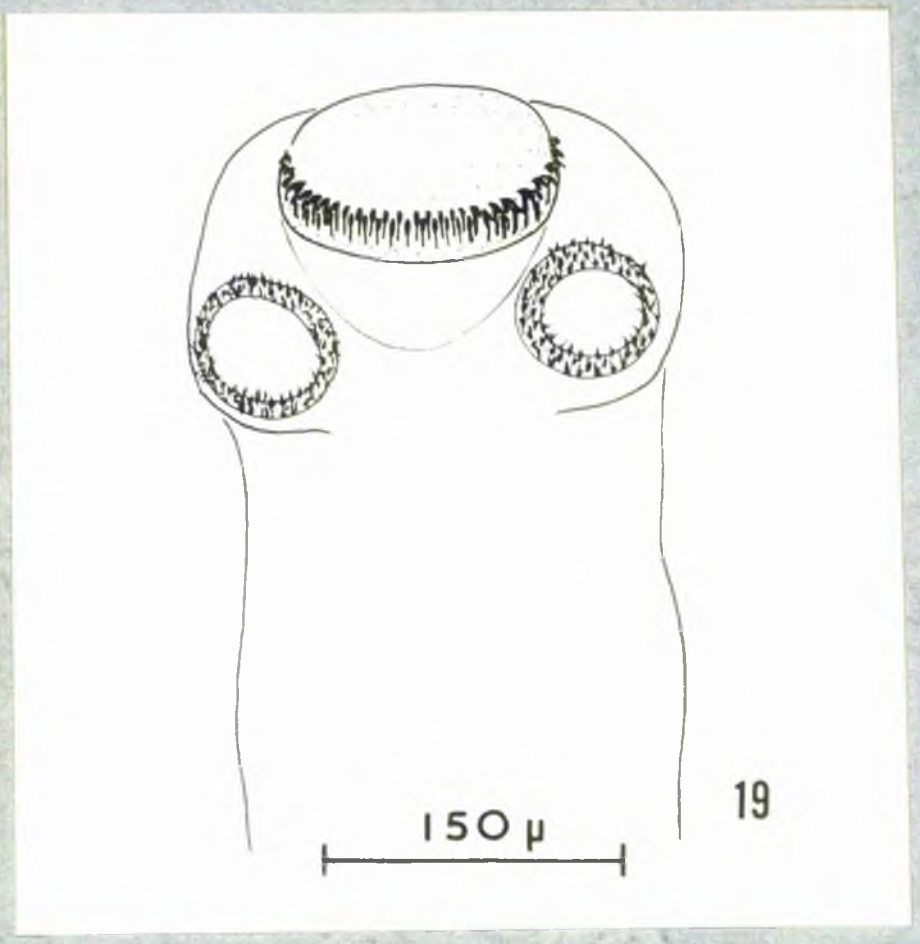


Fig. 19. Raillietina (R.) allomyodes Kotlan, 1921. Scolex.

The scolex (Fig. 19) measures 200μ long by 270μ in diameter and bears a rostellum of 150μ in diameter. The rostellar hooks, which number about 210, are present in a double circlet around the rostellum and are of two distinct sizes: those of the anterior tow measuring 18μ in length and those of the posterior tow measuring 21μ in length. The four suckers are ovoid, measuring 75-85μ by 68-77μ, and are armed with three or four rows of thorn-shaped spines which vary from 5μ to 10μ long.

There are 7-9 testes in each proglottis and in mature proglottides these are 30-50μ in diameter. The cirrus sac, which opens laterally in the anterior half of each proglottis, is 100-130μ long by about 60μ in diameter and contains a cirrus armed with long fine hairs. There is an internal seminal vesicle at the base of the cirrus sac and this measures 20-25μ in diameter. Leading into the seminal vesicle is a highly convoluted vas deferens which runs parallel to the anterior margin of each proglottis.

The ovary is bilobed and is situated centrally in a ventral position. The vitelline gland, which lies immediately posteriorly to the isthmus of the ovary, measures 20-35μ x 90-105μ. There is a distinct swelling of the vagina, adjacent to the genital aperture, which measures 35-45μ x 20-25μ and which probably functions as a receptaculum seminis.

DISCUSSION:

Table VI lists those species of Raillietina which possess rostellar hooks in the range 18-21μ, and which possess less than 20 testes. As is suggested in the discussion following the description of Raillietina (R.) sequens, it seems probable that several of the different species listed may well be intraspecific varieties of a single species. For instance, the only real difference between allomyodes and columbiella lies in the lengths of the cirrus sacs which are 120-150μ and 160-230μ respectively. Without a thorough re-examination of the type material, it is not possible to state that these names are synonymous, but it could well be the case that the cirrus sacs in allomyodes were measured in younger proglottides or, more probably, that the smaller size may be explained in terms of a difference in host species. Similarly, it is quite clear from Table VI that taiwanensis and weissi are similar in most respects differing only in that the former has 14-17 testes while the latter possesses only 12 testes. Looking at the variety weissi valliclusa, however, it is clear that the range quoted for this variety, of 12-15 testes, falls exactly between the ranges for the two species just mentioned. Furthermore, in view of the evidence presented in the discussion on

Species:	filiformis Wigdor, 1920	oligacantha Fuhrmann, 1909	allomyodes Kotlan, 1921	arvensis Fuhrmann, 1911	columbiella Ortlepp, 1938	flaccida Meggitt, 1926	fravi Joyeux & Houdemer, 1927
Description taken from:	Sawada (1964)	Fuhrmann (1909)	Kotlan (1921)	Fuhrmann (1911)	Ortlepp (1938)	Meggitt (1926)	Joyeux & Houdemer (1927)
Strobila (length x max. breadth in mm)	54 x 0.4	50-80 x 1	60 x 0.76	100 x 2	34-67 x 2	130-150 x 1.2	71 x 1.5
Scolex (diameter in µ)	-	370	289	300-38 (=380?)	188-270	-	310-350
Rostellum (diameter in µ)	-	110	-	110	120-180	-	140
Rostellar hooks (number)	90-100	34	160-200	180-200	200	150	350
Rostellar hooks (length in µ)	20-21	21-23	17-18	18	19-22 ♂ 16-18 ♀	17 ♂ 22 ♀	16-18
Suckers (diameter in µ)	-	180	78	90-100	58-80 ♂ 70-90 ♀	-	70-90
Sucker spines (length in µ)	-	-	-	-	up to 10	-	12-15
Testes (number)	10-12	-	12-16	20	11-13	14-17	13
Testes (diameter in µ)	-	-	40	50-60	63-77	-	30-45
Cirrus sac (length x diameter in µ)	-	160 x ?	120-150 x ?	150 x ?	160-230 x 50-87	100 x ?	175 x 50
Eggs (number/capsule)	1	1	6-7	-	4-8	8-9	12
Eggs (diameter in µ)	-	40-48	-	-	-	-	-
Oncospheres (diameter in µ)	-	36	-	-	-	-	12
Genital apertures (arrangement)	Unilateral	Irregularly alternating	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral
Avian host (order)	Columbiformes	Crypturiformes	Columbiformes	Psittaciformes	Columbiformes	Galliformes	Columbiformes

lutzi Parona, 1901	*lutzi* Parona, 1901	*nagpurensis* Moghe, 1925	*cesarinoa nova* Johri, 1934	*permista* Southwell & Lake, 1939	*polychalix* Johri, 1934 (in part.) nec Kotlan, 1920	*taiwanensis* Yamaguti, 1935	*weissi* Joyeux, 1923	*weissi* var. *vallicluse* Joyeux & Baer, 1936	Borneo material
Parona (1901)	Fuhrmann (1909)	Lopez-Neyra (1911)	Johri (1934)	Southwell & Lake (1939)	Johri (1934)	Yamaguti (1935)	Joyeux (1923)	Sawada (1965)	
52-60 x 1 .	60 x 1	250-274 x 1.9	248 x 0.67	30 x 1.5	-	170 x 1.8	142 x 2	140-150 x 2	15 x 0.8
250	470	339-382	250	240	103	240-280	150-170 (& up to 260)	150-170	270
-	70	216-241	-	-	-	150-180	100	100-150	150
-	100	220	154-184	36	190	200	150-300	200-250	210
20	18-19	17-19	14 x 19	18	13.5-19	19	16 x 19	20-25	18 x 21
-	110	142 x 114	-	136	-	60-84	44-60	40-60	75-85 x 68-77
-	-	7	-	-	-	8-10	10	10	5-10
-	-	19-22	16-19	15-20	9-11	14-17	12	12-15	7-9
-	-	72-78	-	-	-	-	60-80	-	30-50
-	-	90-111 x 30-42	125-134 x ?	ca. 105 (from drawing)	61 x ?	100-120 x 28-42	100-130 x 25-40	100-130 x 25-40	100-130 x 60
-	12-16	3-8	5-7	6	-	3-8	6	6	-
-	-	50 x 43	-	-	-	36-42	33-43	43	-
-	-	17 x 14	47-55	-	-	-	18	18	-
Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral
Piciformes	Piciformes	Columbiformes	Passeriformes	Piciformes	Psittaci-formes	Columbiformes	Columbiformes	Columbiformes	Columbiformes

Table VI

Raillietina species with less than 20 testes and with rostellar hooks in the range 18-21 μ

Raillietina (R.) sequens it would appear that the number of testes can show a relatively wide range within a single species and accordingly not only would taiwanensis and weissi be synonymous, but, further, these would simply represent variations of Kotlan's species, allomyodes. Although it is not intended that these, or any others, be united into a single species at the present time, the possibility that a difference in host species may affect differently the morphological development of the infesting worms is obviously a strong possibility which warrants experimental verification.

The present material differs in at least one respect from all the other species described, but in view of the close similarity of allomyodes, taiwanensis and weissi to each other and to the present worms, these are identified as belonging to that group all members of which should, on grounds of priority, be referred to the species allomyodes.

Raillietina (Raillietina) species

Host: Treron curvirostra 9265.

The strobila measures 50 mm long by 1.15 mm in maximum breadth. Nearly all the segments are much broader than long although the last few segments have a tendency to become square or slightly longer than broad. The genital apertures are unilateral and situated in the anterior half of each proglottis.

The scolex is missing.

There are 20-24 testes which measure 45-60μ by 23-37μ and which are situated in two groups on either side of the female genitalia. The group on the aporal side contains more than that on the poral side. The cirrus sac is long and unusually thin, measuring 110-125μ long by only 15-25μ in diameter. No seminal vesicle was seen and in none of the proglottides was the cirrus extruded. The vas deferens lies in large loose coils in the anterior, poral moiety of each proglottis.

The ovary is bilobed, each of the two lobes being digitate, and is situated centrally in the proglottis. The vitelline gland, 37-45μ by 15-23μ, is compact and irregularly lobed, lying immediately behind the ovary.

The uterus breaks down to form about 25 capsules per proglottis which measure 115-150μ by 85-100μ. In each capsule there are 6-9 eggs which measure 28-32μ by 20-25μ while the contained oncospheres are about 14μ in diameter.

DISCUSSION:

Table VII contains those species of Raillietina (Raillietina) which: (a) parasitize birds; (b) possess a number of testes which falls in the range 20-24; and (c) possess a cirrus sac the length of which falls in the range 100-150μ. As can be seen from the table, the present material agrees reasonably well with several species, but does not agree in every respect with any single species. However, in view of the fact that the scolex is missing and in view of the reasonable similarity to several other species this worm has neither been given the status of a new species, nor has it been identified with any existing species.

Species:	trivensis Fuhrmann, 1911	debilis Baylis, 1919	goura Fuhrmann, 1909	grobbeni Böhm, 1925	kantipura Sharma, 1943	korkei Joyeux & Houdemer, 1927	leiopoas Johnst. & Clark, 1948	microcolecina Fuhrmann, 1909	nicholsoni Baer, 1925	nagpurensis Moghe, 1925	nripendra Sharma, 1943	permista Southwell & Lake, 1939	pintneri Klaptocz, 1906	wernari Klaptocz, 1908	Borneo material
Description taken from:	Fuhrmann (1911)	Baylis (1919)	Fuhrmann (1909)	Böhm (1925)	Sharma (1943)	Joyeux & Houdemer (1927)	Jewell (1965)	Fuhrmann (1909)	Baer (1925)	Moghe (1925)	Sharma (1943)	Southwell & Lake (1939)	Lopez-Neyra (1931)	Klaptocz (1908)	
Strobila (length x max. breadth in mm)	100 x 2	45 x 3	170 x 1.1	170-440	160-180 x 0.85	164 x 2	3-6	60-80 x 1	55-60 x 0.82	250-274 x 1.9	200-250 x 1.25	30 x 1.5	35-72 x 1.4	55	50 x 1.15
Scolex (diameter in µ)	300-38 (=380)?	200	180-200	344	220	200	650	380-430	420	339-382	187	240	219	200	
Rostellum (diameter in µ)	110	80	100	96	120	120-130	240-280	200	-	216-241	110	-	42	75	
Rostellar hooks (number)	180-200	enormous number	300	100-200	180-200	150-160	133-154	350	200-240	220	150-180	36	200	200	Scolex missing
Rostellar hooks (length in µ)	18	8	9	13 & 10	20-22	18-20	39-52	-	12.8-13	19 & 17	12	18	6.4-8	-	
Suckers (diameter in µ)	90-100	"	50	125 x 95	55	60-70	160	-	76	142 x 114	62	136	100	30-45	
Sucker spines (length in µ)	"	12	"	7-17	4	up to 10u	6-8	"	8	7	"	"	7-8	7-8	
Testes (number)	20	at least 20	18-20	24-32	16-26	at least 24	22-23	20	14-17	19-22	18-24	15-20	18-20	15-25	20-24
Testes (diameter in µ)	50-60	"	60	54	"	35	"	30-40	40	78 x 72	"	"	40	70-80 x 40-45	45-60 x 23-37
Cirrus sac (length x diameter in µ)	150	125 x 60	120-140	112-117 x 79-84	110 x 48	105-110 x 50	100-130 x 60-70	120	87-114 x 76	90-111 x 30-42	120 x 55	Ca. 100 (from drawing)	100 x 70	100 x 46-58	110-125 x 15-25
Eggs (number/capsule)	"	4-5	8-10	up to 6	3-6	6-9	21-26	8-10	4-6	5-6	4-9	6	15	-	6-9
Eggs (diameter in µ)	-	-	-	-	-	18 x 14	-	-	-	50 x 43	-	-	50	-	28-32 x 20-25
Oncospheres (diameter in µ)	-	15	-	-	-	-	11-14	-	15.2	17 x 14	-	-	19.23	-	14
Genital apertures (arrangement)	Unilateral	"	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral
Avian host (order)	Psittaciformes	Ciconiiformes	Columbiformes	Galliformes	Columbiformes	Columbiformes	Galliformes	Psittaciformes	Columbiformes	Columbiformes	Columbiformes	Piciformes	Galliformes	Coliiformes	Columbiformes

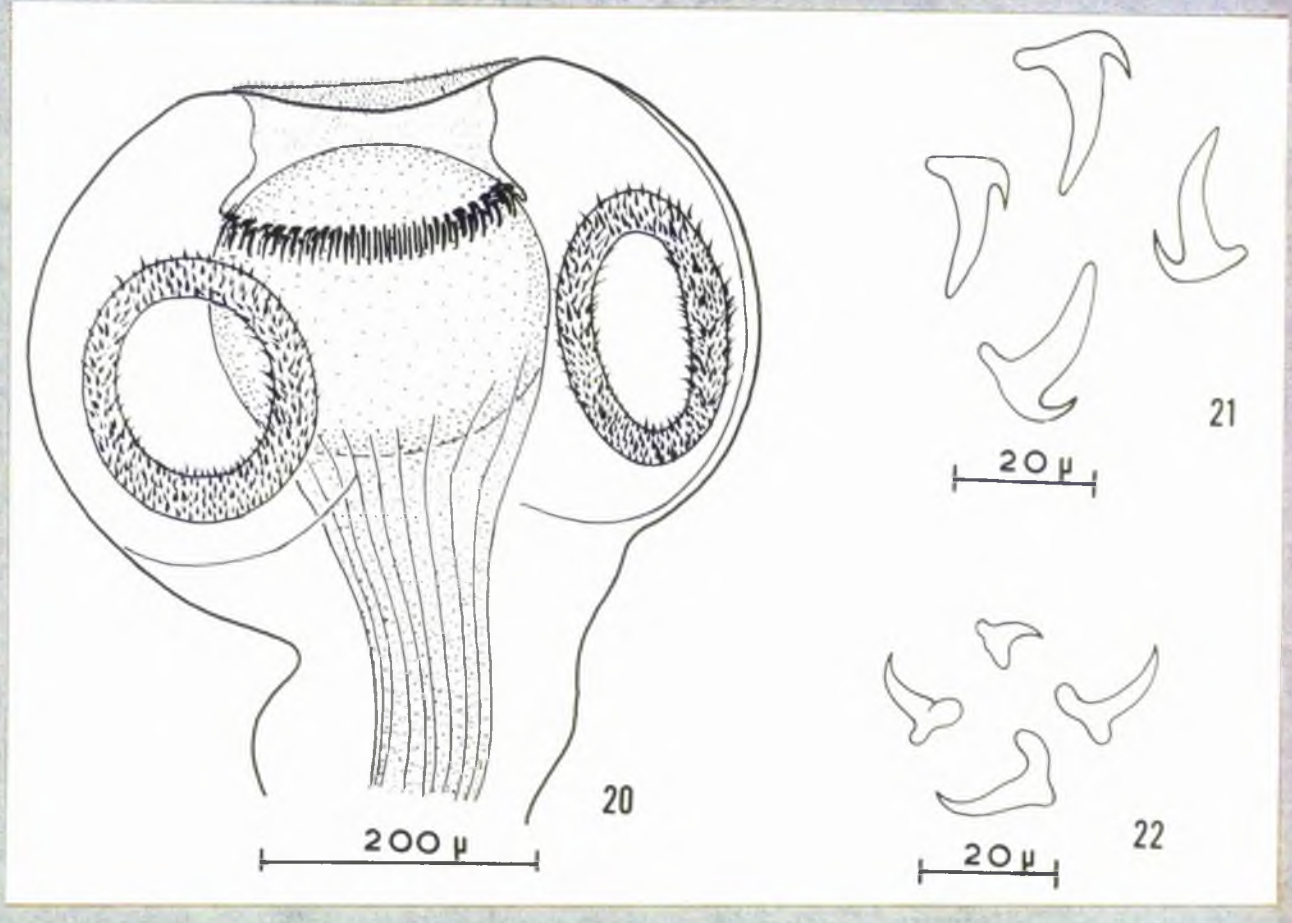
Table VII

Raillietina (Raillietina) species with testes in the range 20-24 and with cirrus sacs in the range 100-150µ in length

Raillietina (Paroniella) siamensis Schmelz, 1941.

Hosts: Megalaema chrysopogon 8750, 8891, 9418;
Meiglyptes tukki 9274;
Charadrius leschenaultii 9486.

The longest specimen is 35 mm and the maximum breadth from any of the worms is 1.15 mm. The proglottides are all broader than long and in mature proglottides the breadth varies from two to four times the length. The genital apertures are unilateral and the genital ducts pass between the dorsal and ventral excretory canals.



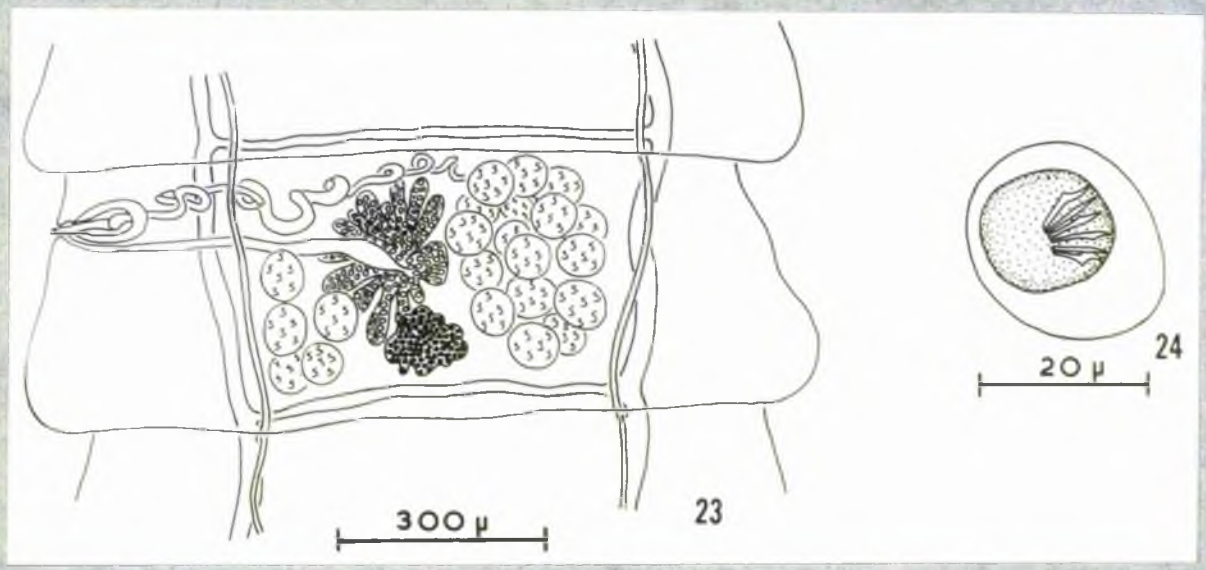
Figs 20-22. Raillietina (Paroniella) siamensis Schmelz, 1941. Scolex (Fig. 20), rostellar hooks (Fig. 21), and sucker spines (Fig. 22).

The scolex (Fig. 20) measures 490-525μ across the region of the suckers and has a length of about 350μ. The rostellum is 174-215μ in diameter by 140-178μ in length and bears a double crown of about 200-300 hammer-shaped hooks (Fig. 21). The hooks in the anterior row are larger than those of the posterior row; the former being about 28μ long while the latter are only 19-23μ long. There are four well-developed suckers, armed with spines (Fig. 22) of 8-18μ in length. In some specimens the anterior part of the scolex could be seen to be covered with hair-like spines less than 3μ long. This was easily seen where the rostellum was invaginated.

There are 20-40 testes (Fig. 23) which lie in two separate fields; the larger group lying aporally comprising 12-30 testes. The testes measure 40-90μ by 37-68μ. The cirrus sac has a length of 90-130μ and a maximum diameter of 60-74μ. It has a thick wall of about 8μ and opens into the genital atrium anteriorly to the opening of the vagina in the anterior half of the lateral margin. There is neither an internal nor an external seminal vesicle, although in fully mature and gravid proglottides, the vas deferens becomes greatly swollen with sperm and may act as an external seminal vesicle. In early proglottides the vas deferens tends

to lie along the anterior edge of the segment but as it becomes filled with sperm, it comes to occupy most of the anterior poral quarter of each proglottis and lies in large loose coils.

The ovary is fanlike and deeply lobed with a maximum breadth of about 300μ and lies ventrally in a median position. The vitelline gland, lying immediately posteriorly and slightly aporally to the ovary, is irregularly ovoid and measures 104-180μ by 65-100μ. The shell gland, with a diameter of about 15μ, lies between the ovary and the vitelline gland. On leaving the genital atrium, the vagina lies parallel to the anterior margin and widens out, before reaching the centre of each proglottis, to form a receptaculum seminis.



Figs 23 and 24. Raillietina (Paroniella) siamensis Schmelz, 1941. Mature proglottis (Fig. 23), and egg with contained oncosphere (Fig. 24).

The uterus can first be seen as a transverse band across the anterior region of the proglottis and it eventually breaks down to form uterine capsules, each of which contains but one egg. The size of the capsules is 34-38μ by 30-32μ; the diameter of the contained eggs (Fig. 24) is 25-27μ by 22-24μ; and the diameter of the embryos is 9-15μ. The oncosphere hooks are small, measuring 7-9μ in length.

DISCUSSION:

As can be seen from Table VIII, the present material agrees closely with that described by Schmelz (1941) as Raillietina (Paroniella) siamensis and also with material described by Johnston (1914) as Davainea sphecotheridis. Schmelz separated his species from that of Johnston on the following grounds:

(a) sphecotheridis is a parasite of Passeriformes whereas siamensis is found in Capitoniformes;

(b) The scolex of sphecotheridis bears a great number of minute spines, particularly at the base of the rostellum, whereas siamensis does not have these;

(c) there are fewer and smaller testes in sphecotheridis than in siamensis;

Species:	Davainea sphecotheridis	Raillietina siamensis	Borneo material
Strobila: (length x max. breadth in mm)	100 x 2	45 x 4.8-4.9	35 x 1.15
Scolex (diameter x length in µ)	360	400-440 x 240	490-525 x 360
Rostellum (diameter x length in µ)	-	130-150	174-215 x 85-150
Rostellar hooks (number)	very great number	240	200-300
Rostellar hooks (length in µ)	ant.row: 20 post.row: 15	ant.row: 24 post.row: 20	ant.row: 28 post.row: 19-23
Suckers (diameter in µ)	140	200	174-215 x 140-178
Sucker spines (length in µ)	up to 10	-	8-18
Testes (number	ca 30	50-60	20-40
Testes (diameter in µ)	25-30 x 15-20	80 x 60	40-90 x 37-68
Cirrus sac (length x diameter in µ)	100 x 40	150-160 x 66-68	90-130 x 60-74
Ovary (shape and size in µ)	digitiform lobes	495	fanlike, deeply lobed; 300
Vitelline gland (shape and size in µ)	solid and rounded	145	irregularly ovoid 104-180 x 65-100
Egg capsule (diameter in µ)	27 x 20 (egg)	30-36	34-38 x 30-32
Embryo (diameter in µ)	17	12-14	9-15

Table VIII

Comparison of Borneo material with
Davainea sphecotheridis and Raillietina siamensis

(d) the rostellar hooks are smaller in sphecotheridis and there appear also to be differences in the length and breadth of the strobila, in the length of the cirrus sac, and in the diameter of the embryo.

However, it is clear from the present material that some of these characters which purportedly separate these species are, in fact, common to both. The minute hooks described by Johnston on the scolex of sphecotheridis are abundantly clear in the present material but only when the rostellum is not evaginated, which would suggest that they are extremely caducous and which might well explain why Schmelz did not see any such spines, although he was looking for them, in his material. The number of testes in the present material seems to fall half-way between the number described for sphecotheridis and the number described for siamensis and it is quite possible that the number of testes is a variable character within the limits quoted. The difference in the sizes of rostellar hooks seems hardly sufficient for this not to be due to measuring technique particularly in view of the fact that when the hooks of the present material were measured from whole mounts in Canada balsam the lengths were considerably lower than those actually recorded from squash preparations in Berlese fluid.

In view of the number of small discrepancies present between the two species, it may be that they are in fact separate species, but the present material suggests that there is a range of variation which may well encompass both described species. However, without examining the type material of *sphecotheridis* and that of *siamensis* it would not be wise to make these two species synonymous and accordingly the present material is tentatively identified as *Raillietina* (*Paroniella*) *siamensis* as it seems to fit Schmelz's description slightly better than that of Johnston but it is strongly suggested here that *siamensis* is a synonym of *sphecotheridis*.

It is probable that there is a mistake in labeling in some of the present material as a Charadriiform bird, namely *Charadrius leschenaultii*, is apparently a host for this species whereas this order of birds has not previously been shown to carry species of *Raillietina* (see discussions following descriptions of *Raillietina* (*R.*) *johri* Ortlepp, 1938 and *Kowalewskiella susanae* n. sp.)

Furthermore, no differences could be found between those worms supposedly from *Charadrius leschenaultii* and those worms from the piciform hosts.

Hymenolepis mahonae n. sp.

Syn.: Hymenolepis fringillarum of Mahon, 1958, nec Rudulphi, 1810.

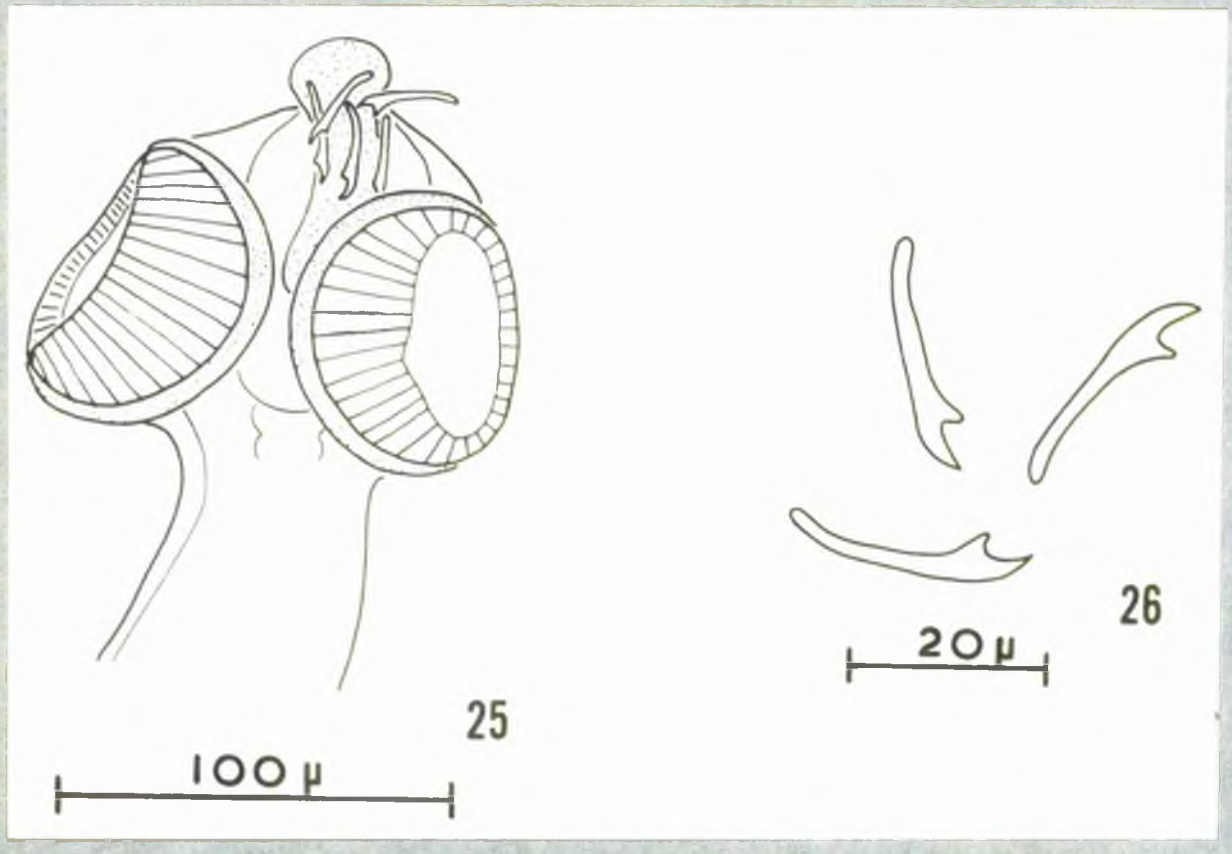
Host: Aegithina tiphia 9045.

There were several worms present only two of which, however, possessed scolices. Of these two, only one (Fig. 25) bore rostellar hooks. The longest complete worm measures 7 mm and has a maximum diameter of 0.5 mm. There are fragments present, however, where the maximum breadth is almost 0.8 mm. The proglottides are all broader than long, the ratio of breadth to length varying from 3:1 to 8:1 depending on the part of the worm. The genital apertures are unilateral and the genital ducts pass dorsally to both the ventral and the dorsal excretory vessels.

The scolex is 96μ long and 140μ in maximum breadth across the widest part. There are four, apparently unarmed, suckers which measure 62-74μ by 50-56μ. The rostellum, 82μ long by 64μ in diameter, bears 10 hooks which are 23-28μ long (Fig. 26).

The three testes are arranged in a triangle (Fig. 27) with one poral and posterior, one aporal and posterior, and one aporal and anterior. The testes measure 60-65μ

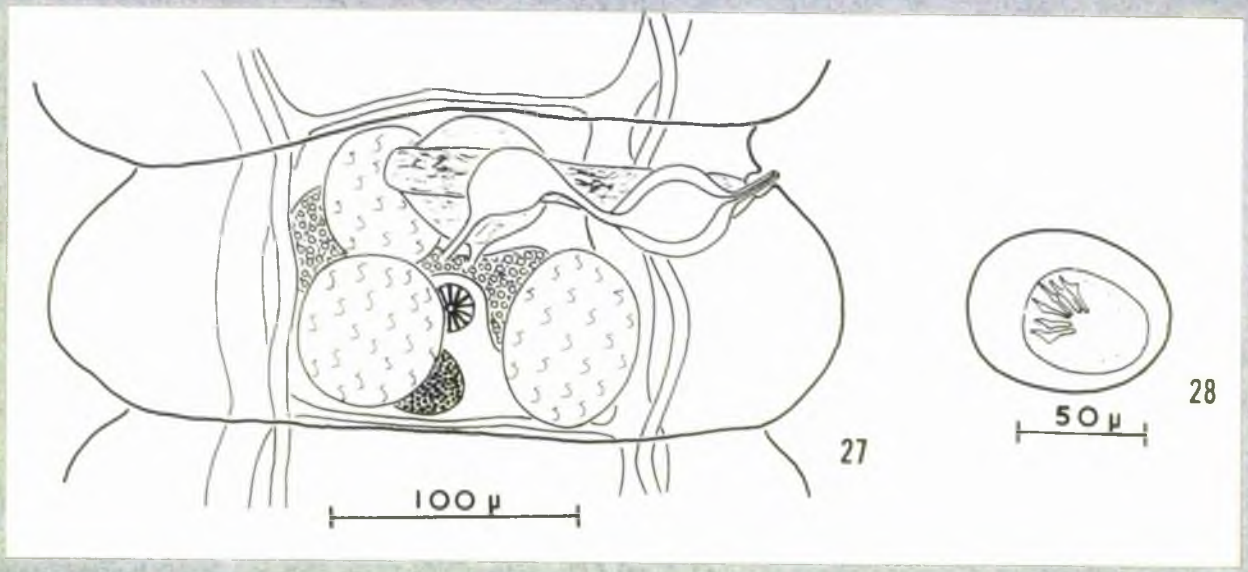
by 49-61μ. There are both an external and an internal seminal vesicle. The external seminal vesicle is 25-35μ in diameter and lies anteriorly about the centre of the proglottis. The internal seminal vesicle is larger and measures 40-50μ in diameter. The cirrus sac was not clearly seen but appears to be about 65-75μ long by about 40μ in diameter.



Figs 25 and 26. Hymenolepis mahonae n. sp. Scolex (Fig. 25), and rostellar hooks (Fig. 26).

The ovary, bilobed and central, measures up to about 200μ across its total width, by 50-80μ. Posterior to the ovary, and lying slightly aporally is the compact vitelline gland which measures 50-55μ by 36-41μ. The

receptaculum seminis lies prominently in the anterior, median portion of each proglottis and, when full of sperm, reaches a size of 52-70μ by 48-55μ.



Figs 27 and 28. Hymenolepis mahonae n. sp. Mature proglottis (Fig. 27), and egg (Fig. 28).

The present specimens are not sufficiently well preserved to allow the elucidation of details of uterus development. The eggs, however, are 42-48μ in diameter (Fig. 28) while the contained oncospheres are 26-32μ by 20-30μ. The hooks of the oncosphere measure 18-20μ in length.

DISCUSSION:

The present material agrees well with material described by Mahon (1958) as Hymenolepis fringillarum (Rudolphi, 1810). Mahon's description, however, does not

agree sufficiently well with the description of Rudolphi (1810), nor with the description of Joyeux and Baer (1936) to allow for its inclusion in the species fringillarum. For purposes of comparison, Mahon includes the figures quoted by Joyeux and Baer in her description and although the scolex in her material has a diameter of less than half that of the worms described by Joyeux and Baer and although the cirrus sac in her material is only a little over half the size of the cirrus sac in the other material, she still identified her material as H. fringillarum (see Table IX). It is proposed here that the worms, identified by Mahon as Hymenolepis fringillarum, in fact are identical with the present material and represent a new species. The new species has been given the patronymic mahonae in honour of Dr. Mahon who first described it. Table X shows all the species of Hymenolepis sensu lato, which possess 10 rostellar hooks, so far recorded from Passeriformes and serves to illustrate the differences between the new species and the other existing species. In order to facilitate comparison of the species, it was thought better to retain the generic term Hymenolepis sensu lato despite the work of Spassky and Spasskaja (1954) and Yamaguti (1959) who have sub-divided this vast genus into many smaller genera employing, unfortunately, what in some cases may be regarded as questionable criteria for creating new genera.

Species:	fringillarum (Rudolphi, 1809)	fringillarum (Mahon, 1958 nec Rudolphi, 1809)	mahonae n. sp.
Description taken from:	Joyeux & Baer (1936) Lopez-Neyra (1942) Mettrick (1958)	Mahon (1958)	
Strobila (length x max. breadth in mm)	32-100 x 0.8-1	-	7 x 0.5(0.8)
Scolex (diameter in µ)	210-300	127-145	140
Rostellar hooks (number)	10	10	10
Rostellar hooks (length in µ)	26-28	26	23-28
Suckers (diameter in µ)	90-100 x 100-120	54-58 x 76-79	50-56 x 62-74
Testes (diameter in µ)	150-170	-	49-61 x 60-65
Cirrus sac (length x diameter in µ)	95-110 x 40	54 x 40	65-75 x 40
Eggs (diameter in µ)	57 x 34	-	42-48
Oncospheres (diameter in µ)	48 x 36	-	26-32 x 20-30
Oncosphere hooks (length in µ)	20	-	18-20
Genital apertures (arrangement)	Unilateral	Unilateral	Unilateral

Table IX

Hymenolepis fringillarum (Rudolphi, 1809) compared with H. fringillarum of Mahon (1958) and present material from Borneo

Species:	farciminosa (Goeze, 1782)	hemignathi (Shipley, 1897)	magniovata (Fuhrmann 1918)	passeris (Gmelin, 1790) =fringillarum (Rudolphi, 1809)	serpentulus (Schrank, 1788)	styposa (Rudolphi, 1809)	zosteropis (Fuhrmann, 1918)	mahonae n. sp.
Description taken from:	Lopez-Neyra (1942) Mettrick (1958)	Shipley (1897)	Lopez-Neyra (1942)	Joyeux & Baer (1936) Lopez-Neyra (1942) Mettrick (1958)	Hughes (1942) Lopez-Neyra (1942) Mettrick (1958)	Hughes (1942) Lopez-Neyra (1942) Mettrick (1958)	Hughes (1942)	?
Strobila (length x max. breadth in mm)	82-120 x 1-1.2	10-22 x 2	25 x 0.4	32-100 x 0.8-1	60-200 x 1.8-2.5	80-110 x 1-1.8	22 x 0.7	? x 0.5(0.8)
Scolex (diameter in μ)	180-265	-	160	210-300	250-350	200-280	200	140
Rostellum (diameter in μ)	100	-	50	-	50	80-100	-	-
Rostellar hooks (number)	10	10	10	10	10	10	10	10
Rostellar hooks (length in μ)	18-24	18-23	30	26-28	18-27	28-38	30-32	23-28
Suckers (diameter in μ)	85-95	-	70	100-120 x 90-100	75-120	85 x 60	88	62-74 x 50-56
Testes (diameter in μ)	90-100	-	-	150-170	150-200	120-150	-	60-65 x 49-61
Cirrus sac (length x diameter in μ)	180-300 x 45	-	100-120 x ?	95-110 x 40	130-190 x 85-110	200-270 x 70-140	120-140 x ?	65-75 x 40
Eggs (diameter in μ)	48-60 x 36-65	40-50	45	57 x 34	110 x 85	-	50-60	42-48
Oncospheres (diameter in μ)	36-48 x 26-30	-	32-36	48 x 36	36-65 x 28-40 (20-24)	40-48 x 32-40	23	26-32 x 20-30
Oncosphere hooks (length in μ)	20	20	-	20	20-22	18-20	-	18-20
Avian host (order)	Passeriformes	Passeriformes	Passeriformes	Passeriformes	Passeriformes	Passeriformes	Passeriformes	Passeriformes

Table X

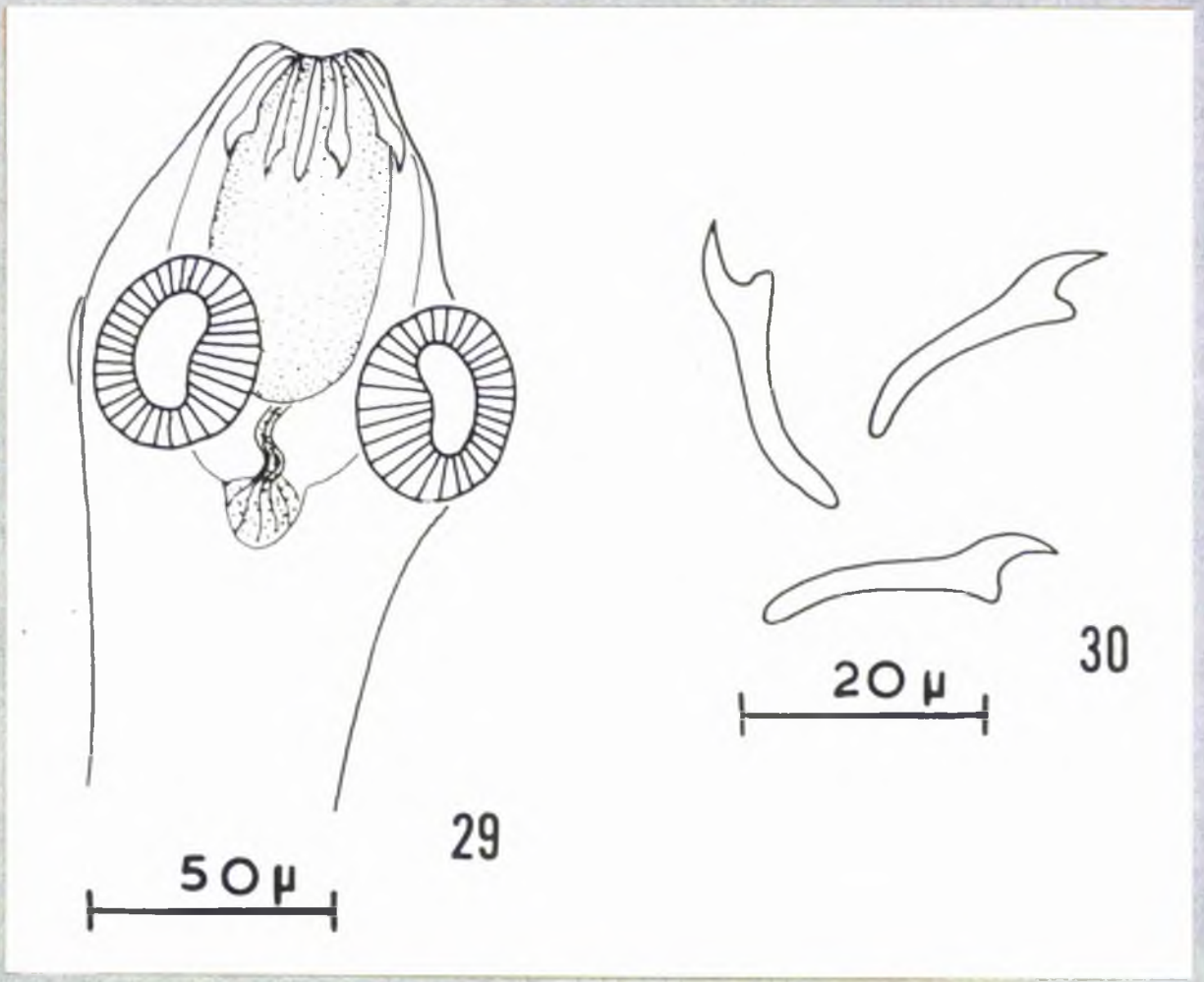
Hymenolepis species with 10 rostellar hooks
within the range 23-30μ long from Passeriformes

It should be mentioned that Spassky and Spasskaja (1954) transferred H. fringillarum to one of their new genera, namely Passerilepis, and Yamaguti (1959) lists fringillarum as a synonym of Passerilepis passeris (Gmelin, 1790). Mettrick (1958), however, redescribed fringillarum retaining both the older generic name of Hymenolepis and also the specific name of fringillarum but he did not discuss any possible synonymy of this worm. Although there may be valid reasons for retaining both specific names fringillarum (Rudolphi, 1810) is listed in Table X with passeris (Gmelin, 1790) in accordance with Ransom (1909) and Yamaguti (1959).

Hymenolepis sp.

Hosts: Anthreptes malacensis 9318, 9358;
Nectarinia calcostetha 9092.

Mature worms measure up to 30 mm long by 0.35-0.46 mm in maximum breadth. The genital apertures are irregularly alternating and the genital ducts pass dorsally to both the longitudinal excretory vessels.

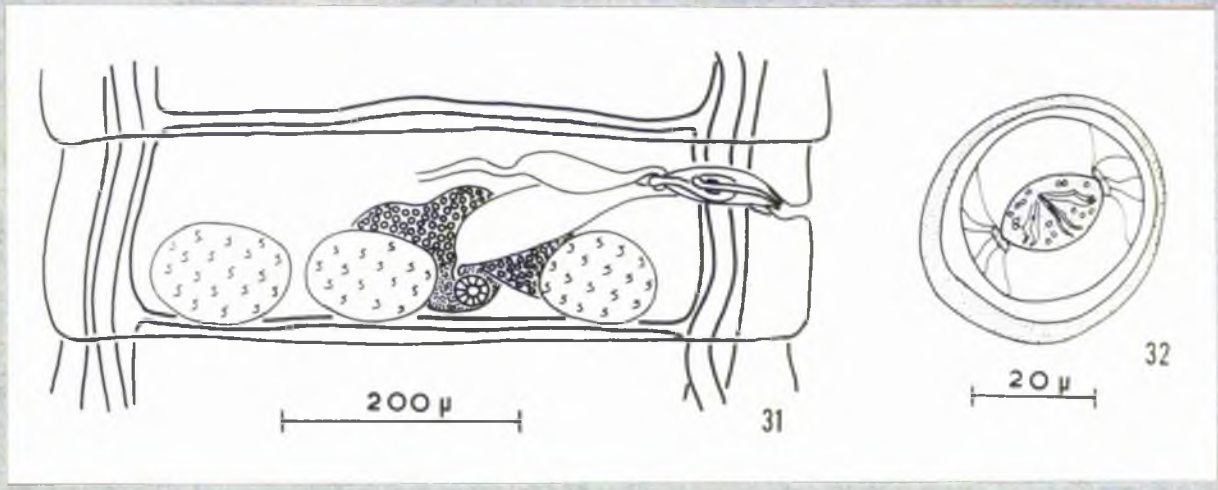


Figs 29 and 30. Hymenolepis sp. Scolex (Fig. 29) and rostellar hooks (Fig. 30).

The scolex (Fig. 29) measures 104-121µ by 115-126µ and bears an armed rostellum and four, apparently

unarmed, suckers. There are 8 hooks (Fig. 30) on the rostellum and these measure 28-36μ long. The suckers are 46-56μ by 33-49μ.

The three testes (Fig. 31) lie in a straight line and when mature, measure 64-110μ by 48-67μ. The cirrus sac is 78-88μ long and has a diameter of 25-33μ. Although the cirrus was not seen in an extruded position, it could be seen lying within the cirrus sac and has a diameter of about 6μ. There are present both an external and an internal seminal vesicle, the latter measuring 21-25μ by 15-23μ. The vas deferens is slightly coiled and lies anteriorly to the cirrus sac, roughly parallel to the anterior edge of the proglottis.



Figs 31 and 32. Hymenolepis sp. Mature proglottis (Fig. 31), and egg with enclosed oncosphere (Fig. 32).

The ovary is distinctly trilobed and lies in the middle of the proglottis. The vitelline gland, lying immediately posteriorly to the ovary, is compact, measures

65-85μ by 43-52μ, and lies ventrally to the middle testis. The receptaculum seminis is large and increases to a maximum size of 163μ by 80μ although in most mature proglottides it measures about 140μ by about 70μ.

There is a sudden transition between mature and gravid proglottides, the eggs being only just visible in the last mature proglottis and filling the whole of the medulla, extending beyond the excretory vessels, in the first gravid proglottis. The eggs (Fig. 32) measure 25-40μ in diameter and the contained oncospheres are 10-14μ in diameter. The hooks of the oncosphere are 7-9μ long.

DISCUSSION:

The present material does not resemble any species listed by Fuhrmann (1932), Lopez-Neyra (1942), or by Yamaguti (1959) as coming from Passeriformes. However, in view of the fact that it has not been possible to examine all the references to *Hymenolepis sensu lato* it was considered advisable not to erect a new species to contain this worm at this time.

Fimbriaria fasciolaris (Pallas, 1781)

Host: Domestic duck (Anas boscas L. dom.) 9575

Specimens are greatly contracted but appear to fit the description by Wolffhügel (1936), who also lists the full synonomy of this species. Webster (1943), in his review of the Fimbriariinae mentions that he found a smaller range in the number of longitudinal muscle bundles in F. fasciolaris than is quoted by Wolffhügel, the former finding only 110-120 in his material whereas Wolffhügel gives the range as 60-120. Although the present material is not well enough preserved for any description, its similarity both to the worms described by Wolffhügel (1936) and to specimens in the Helminthological collection of the British Museum (Natural History) identified as Fimbriaria fasciolaris makes identification reasonably positive.

Paricterotaenia burti Sandeman, 1959

Host: Charadrius leschenaultii 9110

One, small immature worm was present which measured 0.35 mm long by 0.12 mm in maximum breadth. Only two, immature proglottides were present, both being twice as broad as they were long.

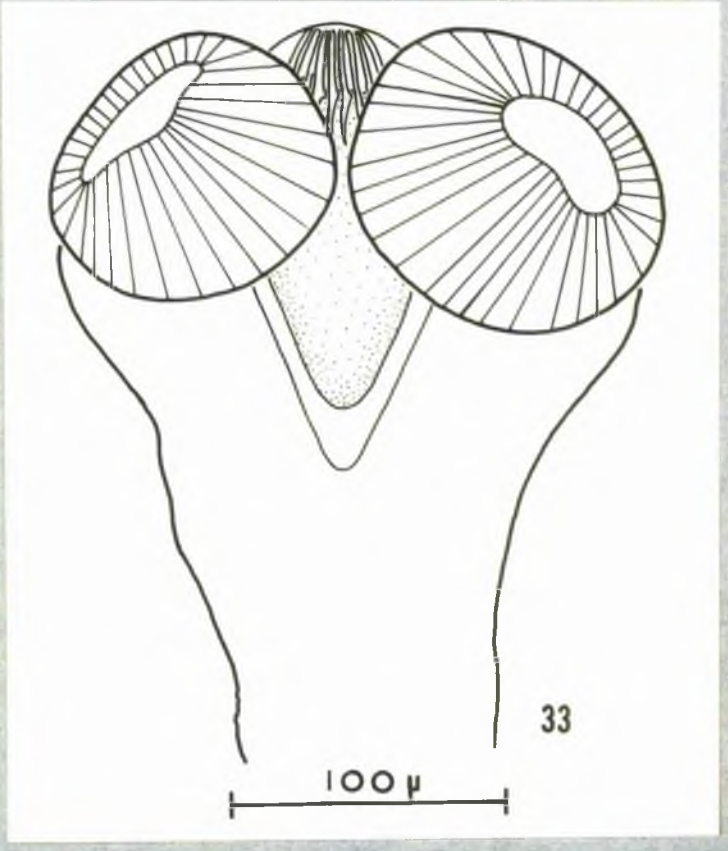


Fig. 33. Paricterotaenia burti Sandeman, 1959. Scolex.

The scolex (Fig. 33) is 200μ by 240μ and possesses four unarmed suckers, 120-140μ by 100-110μ. The rostellum, 150μ long by 70μ in diameter, bears 16 hooks arranged in what appears to be a single row. The hooks are 50-52μ long.

No genitalia were seen at all.

DISCUSSION:

The present material appears to agree sufficiently well with Paricterotaenia burti Sandeman to warrant identification with that species. Sandeman (1959) erected the species to contain worms he found in Lymnocryptes minimus and Numenius arquatus from the River Eden, Fife and also to contain, in part, Paricterotaenia stellifera (Krabbe, 1869). In the original description of P. stellifera Krabbe gives two sets of hook characteristics: one with 10 hooks, 55μ long; and the other with 14 hooks of length 46-51μ. The former set of hook characters is that which has become ascribed to P. stellifera (Krabbe, 1869) while the latter, prior to Sandeman, had been ignored. Hooks of the present material agree closely with those drawn and described by Krabbe and also those described by Sandeman which pertain to P. burti. The measurements of the scolex and rostellum also agree reasonably closely with Sandeman's description and, furthermore, the worms described by Krabbe, by Sandeman, and the present worm were all found in Charadriiformes. This appears to be the first record of this worm in Asia.

Dilepis ardeolae Singh, 1952 (?)

Host: Butorides striatus 9040

The worms are small, measuring up to about 3 mm long by 0.25 mm in maximum breadth. The genital apertures are unilateral.

The scolices are all missing, although several worms are present.

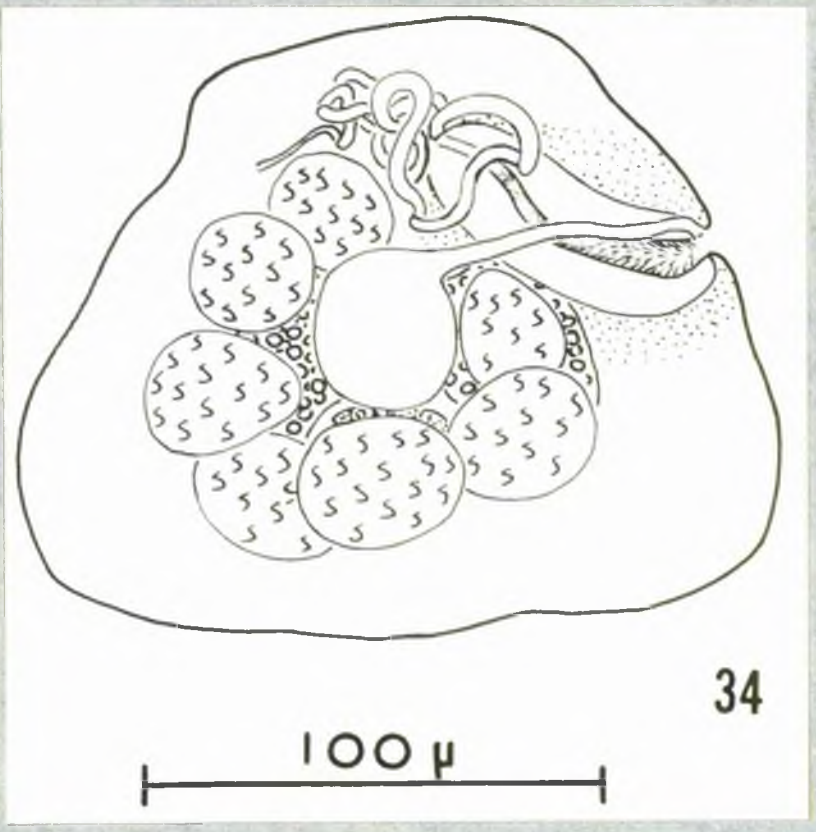


Fig. 34. Dilepis ardeolae Singh, 1952 (?). Mature proglottis.

There are 7 testes (Fig. 34) lying mainly posteriorly and dorsally to the female genitalia and measuring 30-40μ in diameter. In some proglottides, the testes can be seen extending laterally and anteriorly to

the ovary on the aporal side. Neither an internal nor an external seminal vesicle was seen. The cirrus sac, though not seen clearly appears to measure about 80μ long by about 25μ in diameter but this is probably a low figure as there were no gravid proglottides present for comparison. The cirrus is armed but was not seen in the extruded position. In the anterior region of maturing proglottides, the vas deferens becomes profusely coiled and probably serves as an external seminal vesicle when it swells up with sperm.

Lying approximately in the middle of the proglottis is the bilobed ovary, each lobe tending to be more or less spherical. The vitelline gland, lying immediately posteriorly to the ovary, is compact and measures about 30μ by 20μ. In the majority of cases, the vagina opens into the genital atrium posteriorly to the opening of the cirrus sac but this is not constant. Towards the centre of the proglottis the vagina opens into a receptaculum seminis which is broadly fusiform.

DISCUSSION:

The only feature in which the present material differs from that described by Singh (1952) as Dilepis ardeolae is the size of the cirrus sac. In Singh's

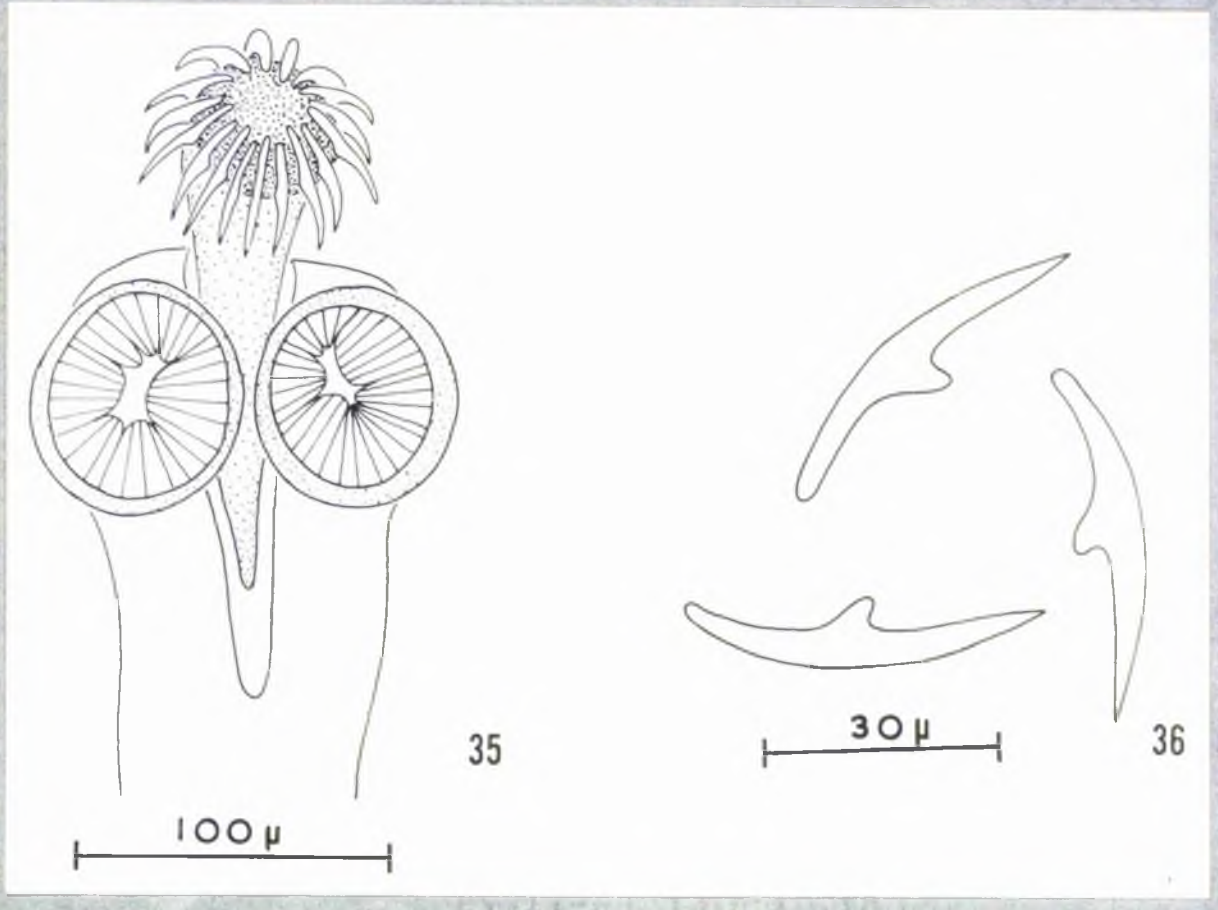
material the length of the cirrus sac is given as 0.248-0.31 mm and the diameter as 0.031-0.037 mm. The cirrus sac in the present material, however, appears to be much smaller being only about 80μ long by 25μ in diameter but as there are no gravid proglottides present it is difficult to state whether the size of cirrus sac measured is the largest size in a complete worm. Despite the apparent discrepancy in size of cirrus sac, the other characters are in such close agreement that the present worms are tentatively identified as Dilepis ardeolae Singh, 1952. Also, the fact that the host Ardeola grayi from which Singh described his species, is closely related both in habitat and phylogenetically to Butorides striatus, the host from which the present material comes, further suggests that the worms may be of the same species.

Liga facile (Meggitt, 1927) Szpotanska, 1931.

Syn.: Anomotaenia facile Meggitt, 1927
Anomotaenia trivialis Meggitt, 1927

Host: Actitis hypoleucos 9196

The worms are very small, not exceeding 1 mm in length, and without exception are immature no genitalia being seen at all. The maximum breadth in all the worms present is the breadth of the scolex across the region of the suckers as in no instance does the breadth of any of the proglottides exceed the breadth of the scolex.



Figs 35 and 36. Liga facile (Meggitt, 1927). Scolex (Fig. 35) and rostellar hooks (Fig. 36).

The scolex (Fig. 35), including the rostellum, measures 160-170μ in length and is 130-150μ broad. The suckers measure 79-82μ by 72-76μ and are unarmed. There are, however, some marks which may be the scars of attachment of acetabular spines along the posterior edge of the suckers. The rostellum, measuring 80-100μ long by 40-60μ in diameter, bears 20 hooks in two alternating rows. The hooks (Fig. 36) in each row are of different sizes: those lying posteriorly measure 41-43μ long, while those lying anteriorly measure 46-51μ long.

DISCUSSION:

The present material differs only slightly from that described by Meggitt (1927) in that the scolex of Meggitt's material is 270μ by 290μ whereas the scolex in the present material is 130-150μ by 160-170μ. In view of the close correlation, however, which obtains in the number and size of the rostellar hooks, the size of the rostellum, the small size of the whole worm; and, furthermore, in the fact that both worms are parasites of wading birds, it seems reasonable to identify the present material as Liga facile (Meggitt, 1927).

Szpotanska (1931) reviewed the genus Liga Weinland, 1857 and transferred Anomotaenia facile Meggitt, 1927 and

A. trivialis Meggitt, 1927 to this genus. She regarded trivialis as a synonym of facile and redescribed the latter species using new material from Burhinus oedicnemus. Sandeman (1959), while accepting that both species belong to the genus Liga, nevertheless regards facile and trivialis, as separate, distinct species but has not yet published his evidence for this view. Williams (1962), however, having examined the type material of both facile and trivialis, supports the view of Szpotanska that the two species are not distinct. On the basis of his comparison of Meggitt's type material with the descriptions of both Meggitt and Szpotanska, he states, in his detailed review of the genus Liga, that there seems to be "scant evidence for regarding A. facile and A. trivialis as distinct species." The main feature of difference between facile and trivialis from Meggitt's description is the size of the rostellar hooks. In A. facile the hooks are 40-50μ long, while in A. trivialis the hooks are 38-39μ long. As can be seen in the present material, however, the hooks in the anterior row are longer than those in the posterior row. Accordingly it is not improbable that Meggitt measured hooks from both rows in the material he described as A. facile, but measured only hooks in the posterior row in the material he described as A. trivialis.

The fact that Williams (1962), on re-examining the type species of A. trivialis, found hooks as long as 45μ supports this postulation. Therefore, there appears to be no justification for regarding facile and trivialis as distinct species.

Anomotaenia depressa (Siebold, 1836) Fuhrmann, 1908

Syn.: Taenia depressa Siebold, 1836
Liga frigida Meggitt, 1927

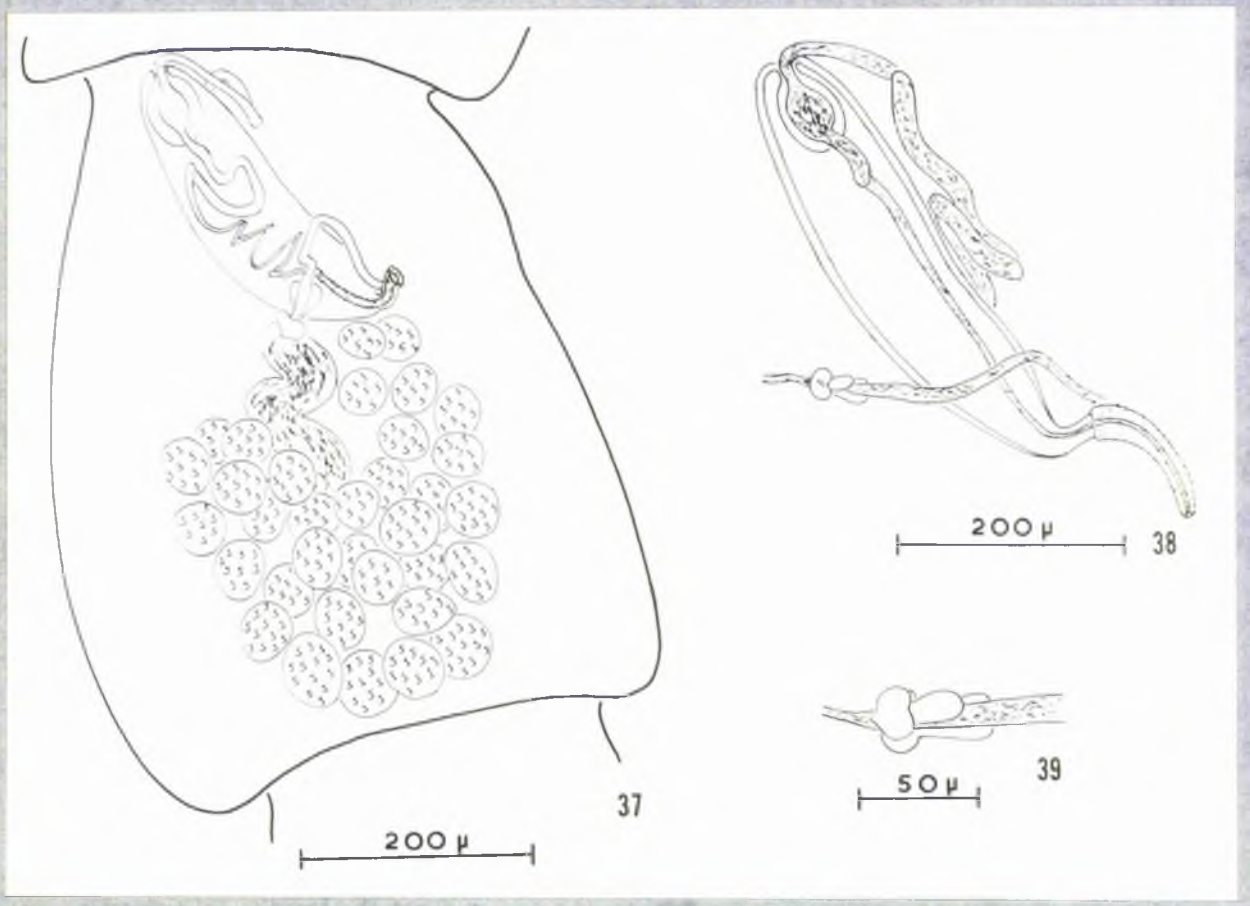
Host: Apus affinis 8784

The present material comprises fragments, all of which probably come from a single worm. The total length of all the fragments is 8 mm and the maximum breadth is 0.6 mm. The immature proglottides at first tend to be rather square in shape but as they mature they become longer than broad. The genital apertures are irregularly alternating.

The scolex is missing.

There are 30-40 testes (Fig. 37) which surround the female genitalia laterally and posteriorly and which measure 40-70μ in diameter. The cirrus sac (Fig. 38) is large, with a length of 400-480μ and a diameter of 80-100μ. The cirrus appears to be fairly short when extruded, having a maximum observed length of 150μ. The diameter of the cirrus base is about 30μ and the diameter of the tip is 12μ. The cirrus is covered for most of its length with fine spines about 4-5μ long. There is no external seminal vesicle present but the vas deferens, on entering the cirrus sac, expands to form an internal seminal vesicle in the proximal part of that organ.

The ductus ejaculatorius is quite narrow and lies convoluted in the distal part of the cirrus sac before entering the cirrus.



Figs 37-39. Anomotaenia depressa (Siebold, 1836). Mature proglottis showing male genitalia and vagina (Fig. 37), cirrus sac and part of the vagina (Fig. 38), and chitinoid vaginal apparatus (Fig. 39).

The deeply lobed ovary is situated posteriorly and ventrally to the cirrus sac which, in some proglottides, overlies part of the ovary. The vitelline gland, lying posteriorly to the ovary and anteriorly to the testes, is irregularly lobular. The vagina has its opening into

the genital atrium posterior to that of the cirrus sac and lies parallel to the cirrus sac until it eventually leads into the recaptaculum seminis through a peculiar, 'chitinoid' structure (Fig. 39). This structure is roughly dumb-bell shaped and has a length of 55-57μ. The diameter of the part closest to the vagina is the same as the diameter of the part next to the recaptaculum seminis and measures 27-29μ. The diameter of the narrow constriction is 8-10μ. The receptaculum seminis, situated immediately behind the cirrus sac and dorsal to the vitelline gland, has a twist in it and when filled with sperm reaches up to 100μ in overall length by about 40μ in diameter.

Gravid proglottides are not present.

DISCUSSION:

Although the scolex is missing and gravid proglottides are not present, this worm is almost certainly the same species as that described by Joyeux and Baer (1936) from Apus apus. Through the kindness of Professor J.G. Baer, I have had a chance to compare the above material with worms from his own collection which he had identified as Anomotaenia depressa and undoubtedly the worms were identical.

The 'chitinoid' structure present at the junction of the vagina and the receptaculum seminis was described by Joyeux and Baer (1936) thus: "Le vagin est entouré, près du réceptacle séminal, d'un manchon cellulaire, auquel fait suite un appareil de fermeture chitineux, à l'entrée de ce réceptacle." In order to measure the structure in the present material accurately, two proglottides were mounted, unstained, in Berlese fluid which rendered most of the tissue transparent. Those structures which showed to advantage after this treatment were the cirrus sac, the narrow portion of the ductus ejaculatorius, the cirrus with its armature of spines, and the structure surrounding the vagina as it enters the receptaculum seminis.

Dollfus (1958), in a footnote on page 515, suggests that the structure may be made of a scleroprotein but that its chemical nature is not known. In the same paper Dollfus reviews those species belonging to the genera Anomotaenia Cohn, 1900; Pseudangularia Burt, 1938; Neoangularia Singh, 1952; and Neoliga Singh, 1952; which possess this structure which he describes as "un appareil occlusif entre le réceptacle séminal et le vagin distal".

Dollfus (1958) discusses fully the complicated synonymy of Anomotaenia depressa (Siebold, 1836) and cites

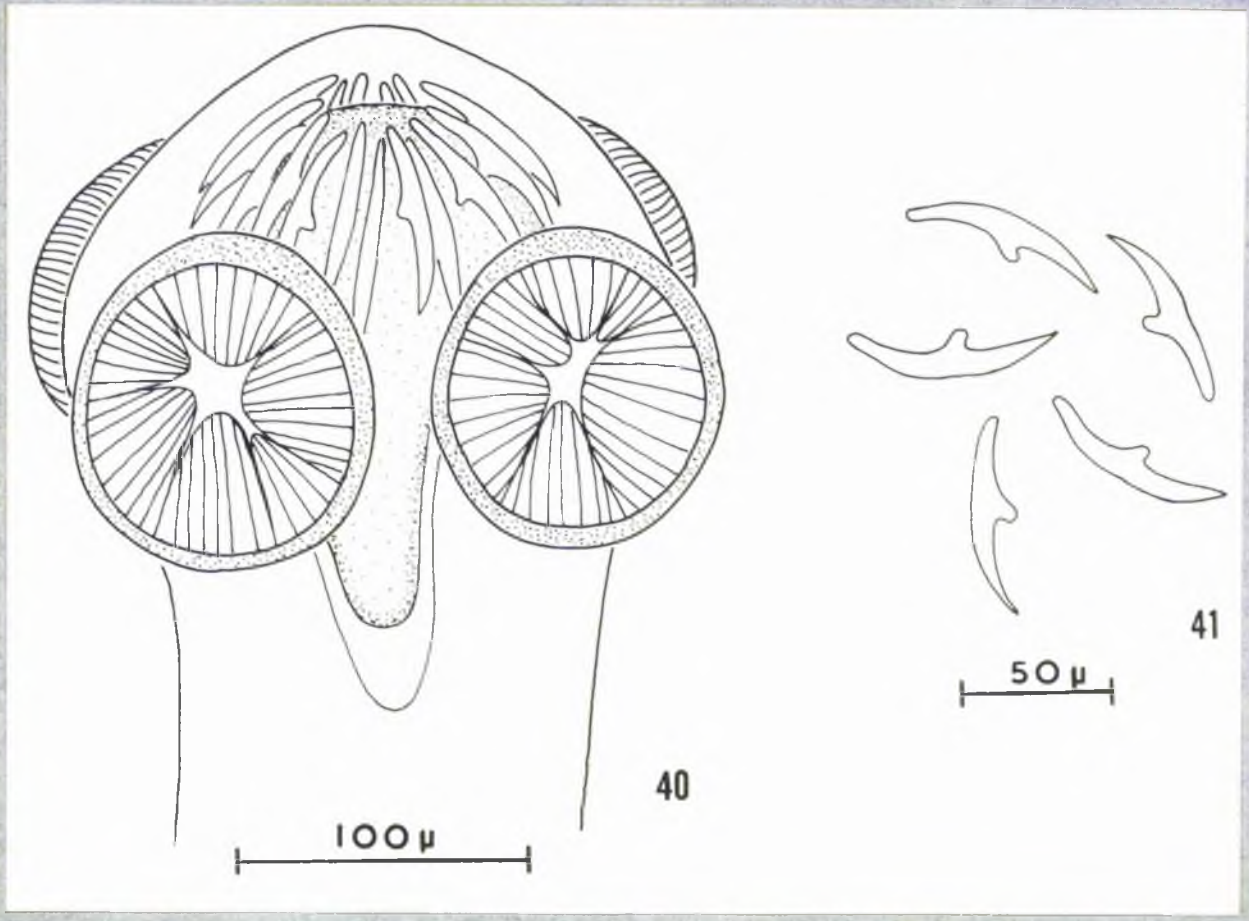
all the descriptions of note. Most of these descriptions are inadequate on their own and accordingly Dollfus gives a compound description which takes into account those given by Krabbe (1869), von Linstow (1896), Fuhrmann (1899), Lopez-Neyra (1923), Joyeux and Timon-David (1934) and which agrees with data taken from his own material. In the resume of his paper Dollfus stresses the insufficiency of present knowledge of both Anomotaenia depressa (Siebold, 1836) and A. cyathiformis (Froelich, 1791) particularly as both these species have been described both from Passeriformes and Cypseliformes. Furthermore, several authors have used, for descriptions of cyathiformis, characters of worms taken from hosts belonging to both these orders. A more recent, though short, description of A. depressa, which agrees with that of Joyeux and Baer (1936), is given by Vojtechovska-Mayerova (1952).

Anomotaenia nymphaea (Schrank, 1790)

Syn.: Taenia nymphaea Schrank, 1790

Host: Numenius phaeopus 9530

Two, small immature worms only were present. Both had complete scolices with full complements of rostellar hooks. A squash preparation was made of one of the scolices while the other was mounted whole in Canada balsam.



Figs 40 and 41. Anomotaenia nymphaea (Schrank, 1790). Scolex (Fig. 40) and rostellar hooks (Fig. 41).

The longer of the two worms measures 0.75 mm with a maximum breadth of 0.110 mm. The scolex (Fig. 40)

is 200μ long, including the length of the rostellar sac, and has a diameter of 250μ. The suckers are ovoid and measure 90-110μ by 80-90μ. No sucker spines were seen. The rostellum is invaginated, measures 200μ from its tip to the posterior extremity of the rostellar sac by 110μ across the broadest part, and carries 20-22 hooks arranged in a double row. The rostellar hooks (Fig. 41) are of two sizes, the larger, lying anteriorly, are 75-80μ long while those in the posterior row are 65-70μ long.

DISCUSSION:

The present material agrees well with material described by Joyeux and Baer (1936) and by Mahon (1958) although Mahon's material was probably in a greater state of relaxation than the present as the diameter of the suckers in her material is considerably greater. Sandeman (1959) has so far been unable to deal with the synonymy of this species but is at present working on this.

Anomotaenia tringae (Burt, 1940) Sandeman, 1959

Syn.: Paricterotaenia tringae Burt, 1940
Anomotaenia paramicrorhyncha Dubinina, 1953

Host: Tringa glareola 9255

The worms measure up to 16 mm long by 0.73 mm in maximum breadth. In immature proglottides the breadth is about twice the length but as the proglottides mature and become gravid, so does the ratio of length to breadth increase until in the gravid proglottides the length is

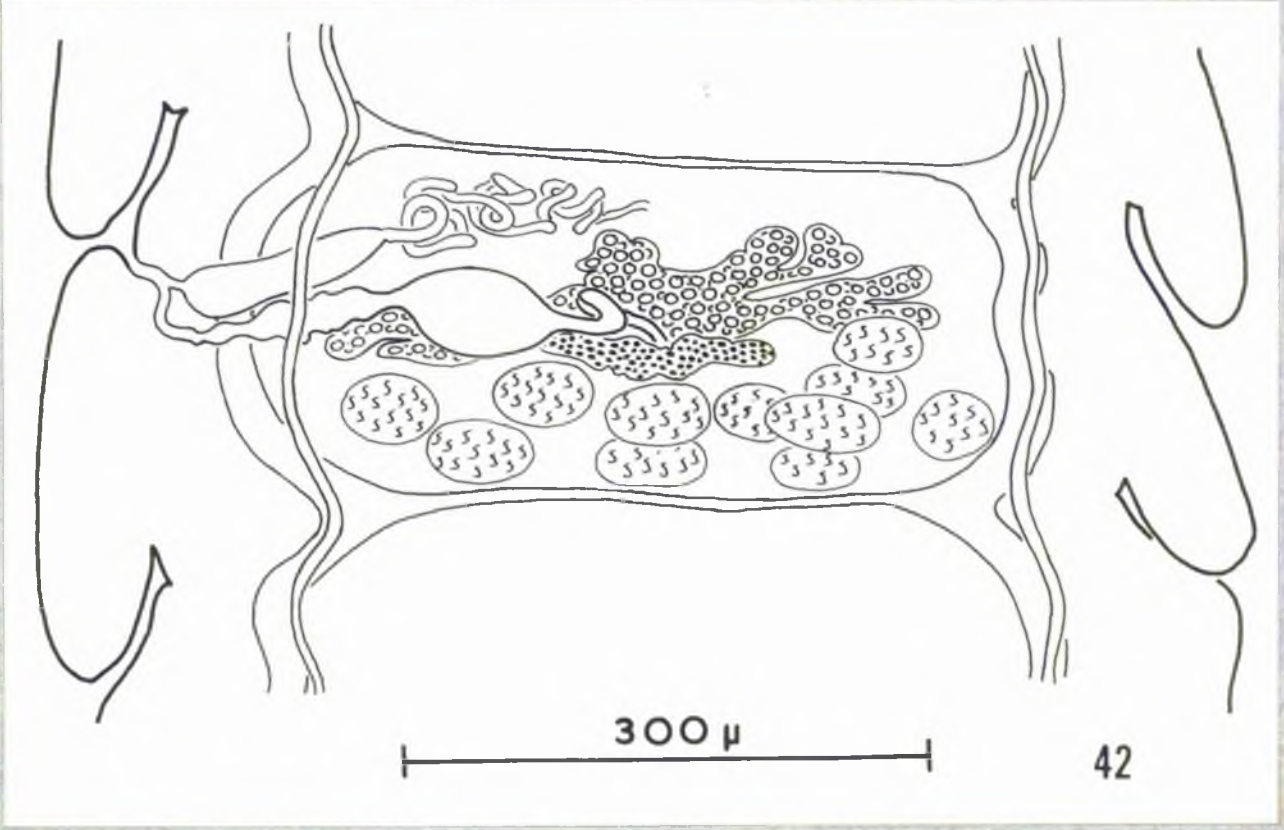


Fig. 42. Anomotaenia tringae (Burt, 1940). Mature proglottis.

about equal to the breadth. The genital apertures are 89% regularly alternating. The genital ducts pass between the dorsal and ventral excretory vessels.

Scolices are not present.

There are 9-11 testes (Fig. 42) most of which lie aporally, and they measure 45-70μ by 25-40μ. There does not appear to be either an internal nor an external seminal vesicle. The cirrus sac measures 87-100μ long by 25-35μ in diameter and has a typical constriction about halfway along its length. In many instances the unarmed cirrus could be seen projecting into the vagina.

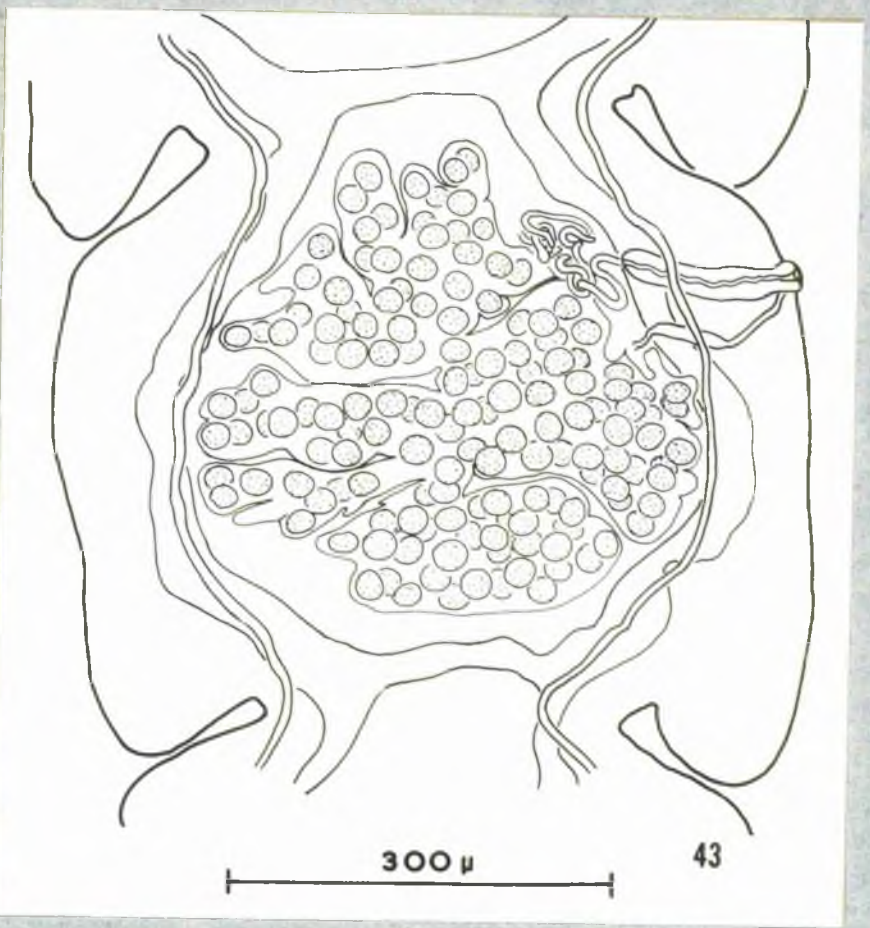


Fig. 43. Anomotaenia tringae (Burt, 1940). Gravid proglottis.

The ovary is irregularly digitate, lies in the anterior third of mature proglottides, and stretches from

the aporal excretory vessels almost to the poral excretory vessels. The slightly lobular vitelline gland lies posteriorly to the ovary but in front of the testes and measures 45-75μ across. Lying to the poral side of the vitelline gland is the receptaculum seminis which is ovoid and measures 59-74μ by 46-64μ when not swollen with sperm, but when swollen, reaches up to 130μ by 70μ.

The uterus is sac-shaped initially, becomes increasingly lobular as the eggs ripen, (Fig. 43) until in fully gravid proglottides, it tends to break down into pseudo uterine capsules. The eggs measure 34-39μ by 31-34μ and the contained oncospheres are 25-30μ by 24-25μ. The hooks of the oncosphere were not fully formed.

DISCUSSION:

The present material agrees well with the type material of Paricterotaenia tringae which Mr. D.R.R. Burt has so kindly placed at my disposal, and with material described by Baer (1959). Despite the fact that the scolex is wanting in the present material, such good correlation obtains through direct comparison of the rest of the anatomy with the type material, that there remains no doubt as to the identity of the present worms. Sandeman, (1959) transfers this species from the genus Paricterotaenia to the genus Anomotaenia. Burt (1940)

states that owing to the fact that there does not exist a dilepid genus with a double crown of hooks and regularly alternating genital apertures "The choice lies therefore between Anomotaenia and Paricterotaenia". Burt chose to place the species in the genus Paricterotaenia on the grounds that the scolex and rostellum are very similar to those seen in several species of Paricterotaenia. The transference of this species to Anomotaenia by Sandeman appears to be purely on the grounds of its possessing a double row of hooks and this is accepted by Baer (1959). Until such a time as Sandeman publishes his larger work on the dilepids of waders, and explains his justification for such a treatment it is probably best to leave this species in the genus Anomotaenia.

Parvitaenia species

Host: Butorides striatus 9040

The worm is incomplete, lacking a scolex. It measures 14 mm in length by 0.9 mm in maximum breadth. The proglottides are all broader than long and the genital apertures are irregularly alternating.

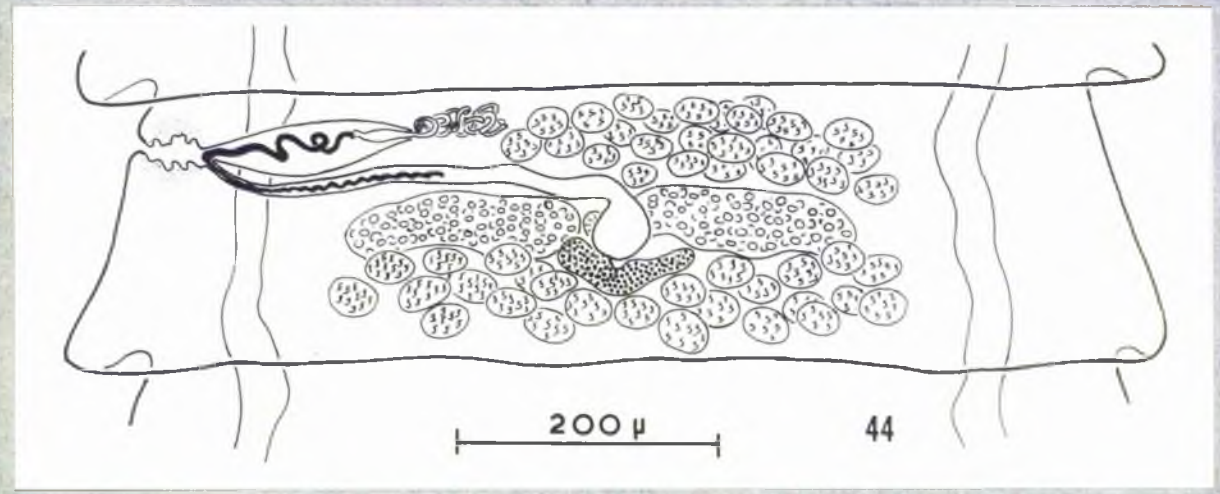


Fig. 44. Parvitaenia sp. Mature proglottis.

There are 50-52 testes (Fig. 44), half lying anteriorly to the female genitalia and half lying posteriorly, which measure 30-50μ by 15-45μ. The cirrus sac is not distinct but appears to be about 115μ long and 45μ in diameter. It lies close to the anterior margin of the proglottis, opening into the genital atrium on the lateral margin. The cirrus is long and in many cases can be seen projecting into the vagina of the same proglottis and reaching almost to the receptaculum seminis.

The ovary is distinctly bilobed, the combined length of both lobes measuring 345-395μ. The vitelline gland, lying more or less in the centre of the proglottis and posterior to the ovary, is irregularly bilobed having a width of 90-110μ. Lying between the ovary and the vitelline gland is the roughly spherical shell gland which has a diameter of about 45μ.

There are no gravid proglottides but in the most mature of those present, eggs can be seen accumulating in the anterior poral part of each proglottis. The parenchyma contains many calcareous corpuscles.

DISCUSSION:

It is not possible to identify this material as to species owing to the lack of a scolex. The internal anatomy, however, strongly suggests that it belongs to the genus Parvitaenia Burt, 1940. Baer and Bona (1960) slightly emend Burt's generic diagnostics and revise the genus to contain 13 valid species: P. ardeolae Burt, 1940; P. macropeos (Wedl. 1855); P. cochlearii Coil, 1950; P. purpurea Johri, 1959; P. magna Baer, 1959; P. macrophallica Baer and Bona, 1960; P. microphallica Baer and Bona, 1960; P. ambigua Baer and Bona, 1960; P. ardeae (Johnston, 1911); P. glandularis (Fuhrmann, 1905); P. aurita (Rudolphi, 1819);

P. clavipera Baer and Bona, 1960; and P. pseudocyclorchida Baer and Bona, 1960. Of these, five are new species and four are new combinations. The full descriptions of the new species are to be given at a later date and until such time as these descriptions appear, simply allocating the present material to the genus Parvitaenia should suffice.

Vitta rustica (Neslobinsky, 1911) Baer, 1959

Syn.: Anomotaenia rustica Neslobinsky, 1911
Vitta magniuncinata Burt, 1938

Host: Hirundo rustica 9202.

The strobila measures 25 mm long by 2.5 mm in maximum breadth. The proglottides are all broader than long, the ratio of breadth to length varying from 3:1 to 5:1 depending both on the state of contraction of the worm and on the site of the proglottis within the strobila. The genital apertures are irregularly alternating and situated laterally, close to the anterior margin of each proglottis, while the genital ducts pass dorsally to both the ventral and dorsal excretory vessels.

The scolex (Fig. 45) has a diameter of 370μ and a length, including the length of the rostellum, of 330μ. The suckers are 73-81μ by 67-79μ and are unarmed. The rostellum, 185μ long by 165μ in diameter, bears 42-45 hooks arranged in two rows in such a way that for every one hook in the anterior row, there are two hooks in the posterior row. The hooks are 50-60μ long, those hooks in the posterior row being slightly longer than those of the anterior row.

There are 60-90 testes (Fig. 46) which, when fully developed, measure 62-77μ by 60-67μ and which are

arranged posteriorly and laterally to the vitelline gland and dorsally to the ovary. There is no external seminal

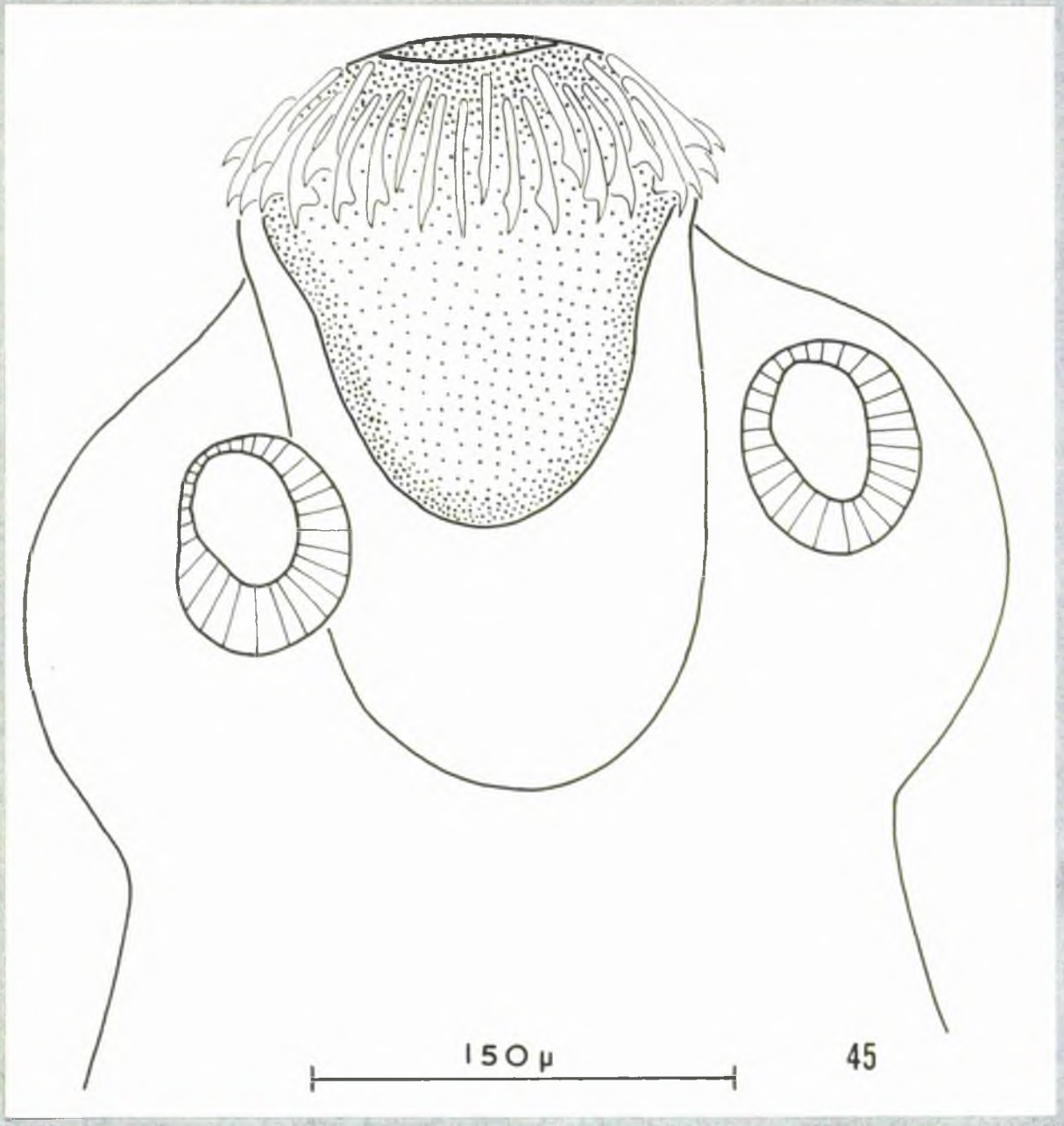


Fig. 45. Vitta rustica (Neslobinsky, 1911). Scolex.

vesicle as such, but the vas deferens expands in the region of the cirrus sac and lies in large loose coils which function as an external seminal vesicle. On

entering the cirrus sac, the vas deferens forms an internal seminal vesicle. The cirrus sac, lying parallel and close to the anterior margin of the proglottis, measures 320-360μ long by 65-85μ in diameter.

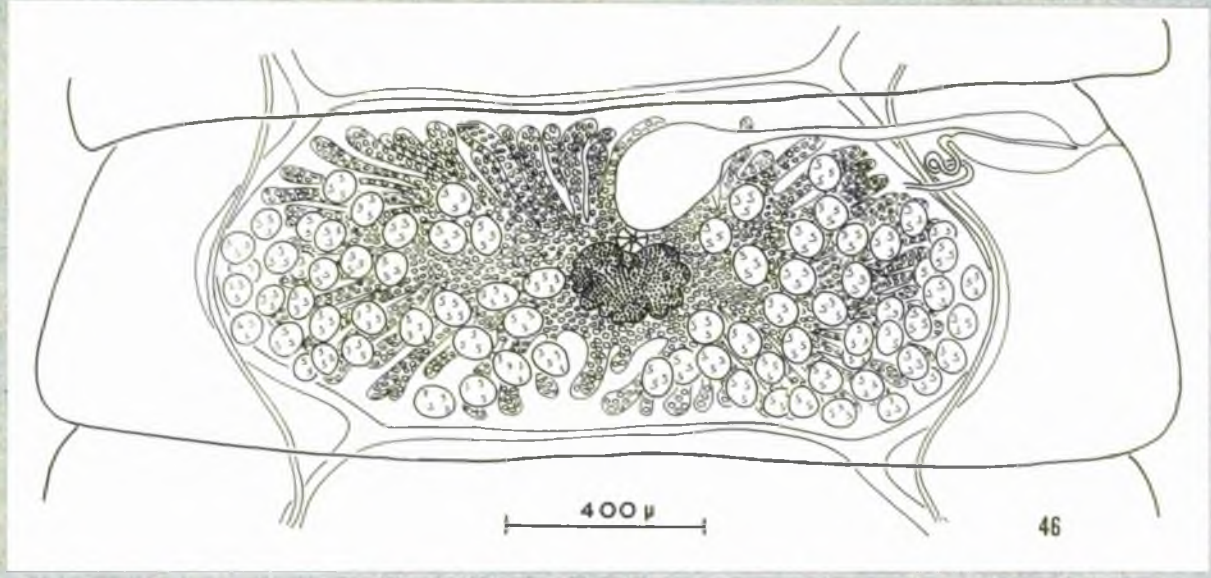


Fig. 46. Vitta rustica (Neslobinsky, 1911). Mature proglottis.

The ovary is bilobed, each lobe being fan-like and divided into a great number of smaller lobes which reach the excretory vessels on both sides of the proglottis. The vitelline gland is U-shaped and measures 90-110μ by 50-70μ. Situated dorsally and slightly anteriorly to the vitelline gland is a well defined shell gland, 45μ in diameter. In the more mature proglottides, the receptaculum becomes quite swollen, often exceeding the size of the cirrus sac.

DISCUSSION:

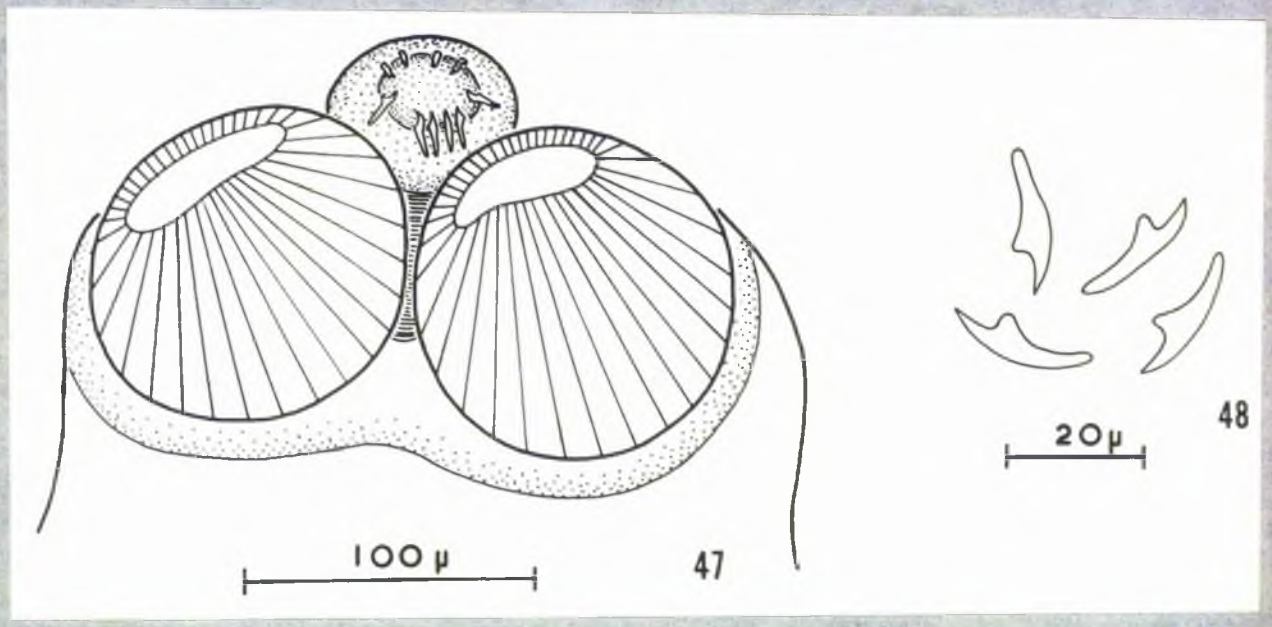
The above material agrees well with that described by Burt (1938) as Vitta magniuncinata and with that described by Baer (1959) as V. rustica. The genus Vitta was created by Burt (1938) to contain two different worms taken from Hirundo rustica gutteralis Scop., 1786, namely magniuncinata and minutiuncinata. The genus closely resembles Anomotaenia Cohn, the main feature of difference being that in Anomotaenia the genital ducts pass between the excretory vessels whereas in Vitta they pass dorsal to both. Baer (1959) transfers Anomotaenia rustica Neslobinsky, 1911, to the genus Vitta and places magniuncinata as a synonym of rustica. He also provides a key to the four species of Vitta which he recognises, using only the characters of hook number and size, and number of testes. These four valid species are: V. parvirostris (Krabbe, 1869); V. minutiuncinata Burt, 1938; V. undulatoides (Fuhrmann, 1908); and V. rustica (Neslobinsky, 1911).

Yamaguti (1959) includes Vitta as a synonym of Angularella Strand, 1928, but gives no indication as to what grounds he has for this. The diagnostic characters of the genera differ essentially in the arrangement of the rostellar hooks. In Vitta there is a double row, whereas in Angularella there is a single row. On this basis, it is proposed to retain, as valid, the genus Vitta Burt, 1938.

Family: Dilepididae

Host: Cacomantis merulinus 9503.

The strobila measures 3.5 mm long by 0.7 mm in maximum breadth. The genital apertures are unilateral. The worm is in a poor state of preservation and did not stain well.



Figs 47 and 48. Dilepid. Scolex (Fig. 47), and rostellar hooks (Fig. 48).

The scolex (Fig. 47) is 160µ long, including the length of the rostellum, by 260µ broad across the suckers. The four suckers are circular in outline and measure 100-110µ in diameter. Sucker spines were not seen. The rostellum, 65µ long and 45µ in diameter, bears a single row of 10 hooks which are not evenly spaced round the periphery therefore suggesting that there may have

been some hooks lost. The length of the hooks is 18-19μ and their shape can best be seen in Fig. 48.

The only genitalia that can be made out with any certainty are the testes which number 24-30 and which measure 45-75μ by 23-38μ. In one segment, there was a suggestion of double genitalia but this clearly was not the normal arrangement.

DISCUSSION:

The worms show many features of the Dilepididae but could belong to a wide range of genera. But for the shape of hooks, the data available from this worm agree very closely with those of Anomotaenia mutabilis (Rudolphi, 1819) Fuhrmann, 1908, even as to the order of host it infests. Owing to the lack of mature and gravid proglottides which can be described, identification further than the family is not possible.

Kowalewskiella susanae n. sp.

Host: Tringa glareola 9255.

Several worms are present in a good state of preservation. They measure up to 25 mm long by 0.525 mm in maximum breadth. The immature proglottides are slightly broader than long but the mature proglottides become twice as long as they are broad. The genital apertures are irregularly alternating. The genital ducts pass between the dorsal and ventral excretory vessels.

The scolex measures 90-100μ in diameter but is bent and squashed so that the length cannot be measured accurately. The suckers are about 45μ in diameter, but these too are squashed. Only three hooks were seen on the rostellum, of which only one could be measured, its length being about 8μ.

There are 21-30 testes (Fig. 49) arranged in two groups, one group lying anteriorly to the female genitalia and the other lying posteriorly. The number of testes in each group is approximately equal and the size of the testes is subject to wide variation measuring 45-65μ by 35-60μ. There is neither an internal nor an external seminal vesicle present, the vas deferens,

however, probably acts as an external seminal vesicle as it becomes greatly swollen with sperm in mature proglottides. The cirrus sac is 92-98μ long by 53-60μ in diameter and is situated laterally, in about the middle

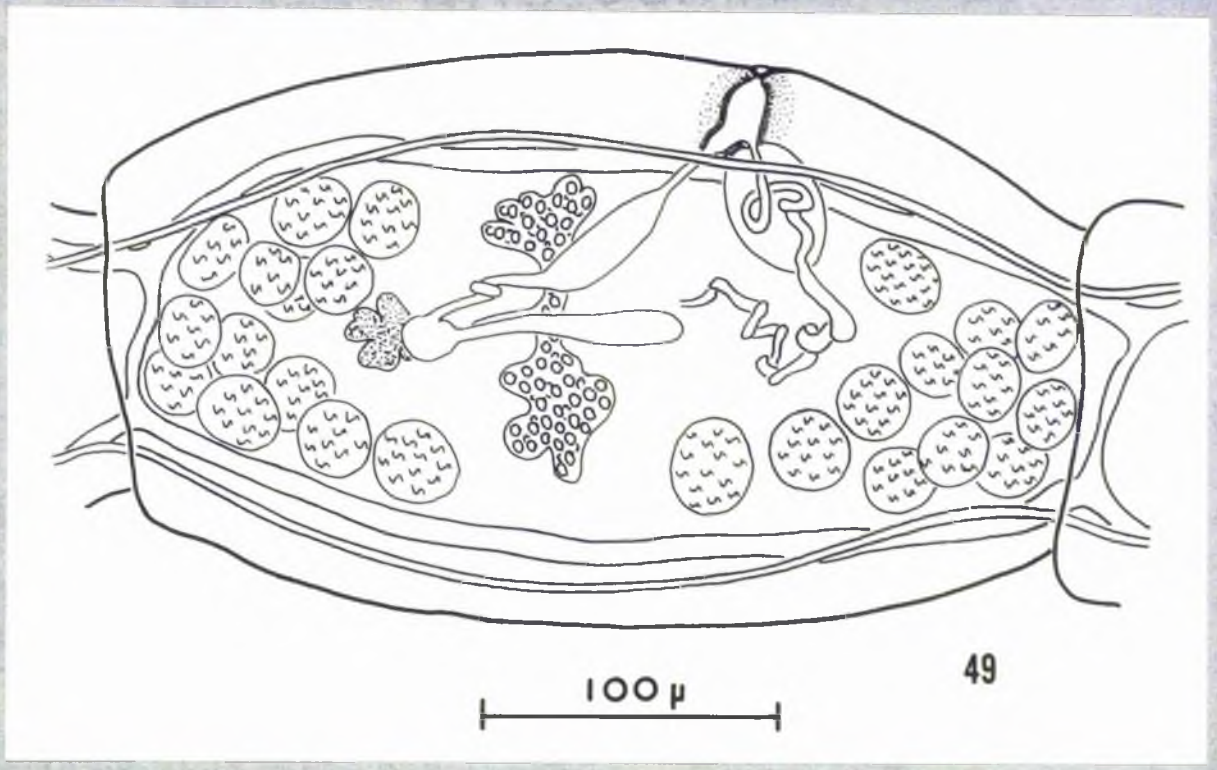


Fig. 49. Kowalewskiella susanae n. sp. Mature proglottis.

of the proglottis. It opens into a well developed genital atrium. In the mounted material, the cirrus is present only as a short papilla but there is a convoluted ductus ejaculatorius still present in the cirrus sac.

The ovary is distinctly bilobed, each lobe being separated by a relatively long isthmus. The lobes

are irregularly lobular and in proglottides where the cirrus sac is well developed, the total breadth of the ovary is 150-250μ. The vitelline gland, lying posteriorly to the ovary, measures 55-90μ by 34-52μ. Just in front of the vitelline gland, but dorsal to it and behind the ovary, is the shell gland which has a diameter of 20-25μ. The receptaculum seminis lies between the cirrus sac and the ovary and shows wide variation in size depending on the quantity of sperm present, the normal variation being 60-90μ by 40-50μ.

Gravid proglottides were not found.

DISCUSSION:

The present material agrees well with material from the same host described by Baer (1959) as Kowalewskiella cingulifera (Krabbe, 1869) Sandeman, 1959. Sandeman (1959) re-erects the genus Kowalewskiella Baczynska, 1914, to contain all those species in which the testes are divided into two groups, one anterior to the female genitalia, and the other posterior. In accordance with this, he transfers Choanotaenia glareolae Burt, 1940, Choanotaenia stagnatilidis Burt, 1940, and Choanotaenia hypoleucia Singh, 1952, all to the genus Kowalewskiella. Furthermore, despite the differences apparently inherent

between these species and Krabbe's species cingulifera, he regards them all, as well as Kowalewskiella longi-annulata Bacyznska, 1914, as synonyms of cingulifera. Baer (1959) accepts this view and in a personal communication points out that "K. cingulifera forms a group within which variations appear to be considerable." This assumption is presumably based on the fact that Baer (1959) described some worms from Tringa glareola, from the Belgian Congo, as K. cingulifera. As can be seen from the accompanying table (Table XI) if Baer's material is, in fact, cingulifera then there would be present very great variation within the species; more variation than can be readily be accepted as existing in any one species. If the two species of Burt (1940), the species described by Singh (1952) and that of Baczynska (1914), are also considered as cingulifera, then this increases the already wide variation even more. Sandeman (1959) does not outline his reasons for placing these various worms in synonymy with cingulifera, but it is doubtful if this sweeping treatment is justified in the present circumstances and, accordingly, it is here suggested that cingulifera, longiannulata, glareolae, stagnatilidis and hypoleucia are all separate species.

Species:	*cingulifera* (Krabbe, 1869)	*longiannulata* (Baczynska, 1914)	*glareolae* (Burt, 1940)	*stagnatilidis* (Burt, 1940)	*hypoleucia* (Singh, 1952)	*bodkini* (Vevers, 1923)	*bodkini* (Vevers, 1923)	*buzzardia* (Tubangui & Masilungan 1937)	*cingulifera* (Baer, 1959 nec Krabbe, 1869)	*susanae* n. sp.
Description taken from:	Krabbe (1869)	Baczynska (1914)	Burt (1940)	Burt (1940)	Singh (1952)	Vevers (1923)	Personal measurements of co-type material	Tubangui & Masilungan (1937)	Baer (1959)	
Strobila (length x max. breadth in mm)	100 x 1	30-40 x 0.54	39-41 x 0.66-0.83	70-120 x 1.15-1.3	35-40 x 0.42-0.46	50 x ?	38-48 x 1.2	160 x 1.9	35 x 0.57	25 x 0.525
Scolex (diameter in μ)	-	65	95	98-100	480-630 (=48-63?)	135	108-136	400	91	90-100
Rostellum (diameter in μ)	-	3.9 (=39?)	37-46	41	43-56	50	48-55	130	-	-
Rostellar hooks (number)	ca. 40	28-30	36-40 (calculated)	28	26	36	-	10	30	-
Rostellar hooks (length in μ)	4-5	52-60 (=5.2-60?)	7	6	6-7	6	-	61-65	8-9	8
Suckers (diameter in μ)	-	23	27-35	37	43-52	50	30-55	120	41	45
Testes (number)	-	ca. 52	30-40	50-62	35-50	45-50	35-54	30	21-31	21-30
Cirrus sac (length x diameter in μ)	-	93.6 x 46.8	188-222 x 62-70	170-204 x 48-60	215-279 x 64-73	(120 x ? 60)	105-130 x 40-72	400 x 100	119 x 61	92-98 x 53-60
Receptaculum seminis (length x diameter in μ)	-	96 x 46	250-275 x 140-155	196-210 x 75-108	189 x 146	150 x 70	120-150 x 120-150	enlarged	large	60-90 x 40-50
Host	*Totanus calidris*	*Totanus stagnalis*	*Tringa glareola*	*Tringa stagnatilis*	*Tringa hypoleucos*	*Actitis macularia*	*Actitis macularia*	*Butastur indicus*	*Tringa glareola*	*Tringa glareola*

Table XI

Comparison of known species of *Kowalewskiella* with *K. susanae* n. sp. from Borneo.

To these five valid species should also be added Kowalewskiella bodkini (Vevers, 1923) n. comb. (=Raillietina (Skrjabinia) bodkini Vevers, 1923), K. buzzardia Tubangui and Masilungan, 1937, and K. susanae n. sp. It is unfortunate that Krabbe's original description is not more complete but it can be differentiated from any of the others on the large size of the scolex, and the large number of rostellar hooks. K. longiannulata can be distinguished from the rest by the fact that it has a small scolex, small cirrus sac, but many testes. The two species described by Burt (1940) are well separated on the constant difference in number of testes and in view of the fact that the cirrus sac in glareolae appears to be significantly larger than that in stagnatilidis even though the outside lower limit of the former overlaps with the upper limit of the latter. Singh (1952), describes the scolex of hypoleucia as 0.634-0.672 mm by 0.48-0.63 mm These measurements, however, are at variance with the figure he draws and the difference does not seem to be merely a matter of a factor of 10. The suckers are described as 0.043-0.052 mm in diameter while the diameter of the scolex is, as stated above, 0.48-0.63 mm. In his drawing, Singh figures four suckers on the scolex and the sizes of the suckers drawn are such that it would

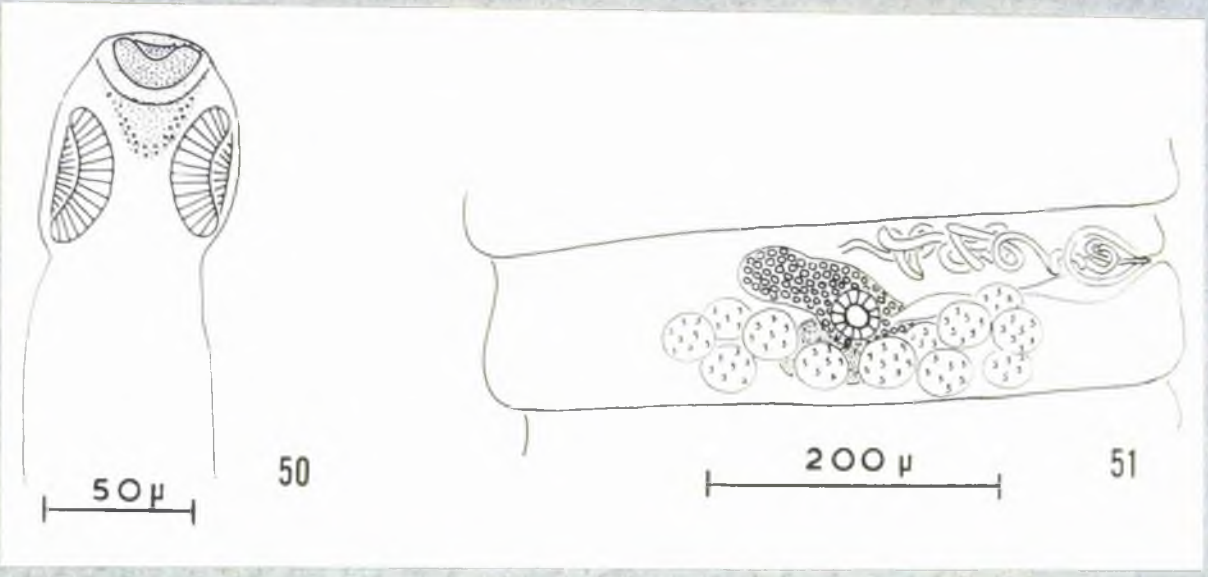
be possible to place three suckers, side by side, and still not project beyond the side of the scolex. Thus, the scolex diameter must be about 130μ or 0.130 mm. According to the scale given, the breadth of the scolex across the suckers is about 110μ. Thus, it seems unlikely that the measurements given by Singh refer to the scolex of this species at all and should probably be completely ignored. However, the large size of the cirrus sac and the large number of testes all serve to separate it from any of the other species. K. bodkini resembles both glareola and stagnatilidis in many respects, but can be separated from both species on account of the size of the cirrus sac. In bodkini, even the largest cirrus sac present, which was measured personally from the type and co-type material, is still 40μ smaller than the lower limit quoted by Burt (1940) for stagnatilidis. Finally, the small number of testes in susanae n. sp. serves to separate it from any of the other species. The small cirrus sac also separates it from glareolae, stagnatilidis and hypoleucia.

The new species described above has been named susanae in grateful recognition of the help received from Miss Susan Burt in the preparation of this manuscript.

Ascometra (?) sp.

Host: Centropus toulou 8927

The strobila measures 55 mm long by 0.9 mm in maximum breadth. The immature and mature proglottides are up to three times as broad as they are long while the length of the gravid proglottides is up to twice the breadth. The genital aperatures are almost unilateral, only 5% of the apertures occurring on the other side. The apertures in this 5% all occur singly.



Figs 50 and 51. Ascometra (?) sp. Scolex (Fig. 50) and mature proglottis (Fig. 51).

The scolex (Fig. 50) is 82µ long and 62µ in diameter. There may be four suckers present, but the only two seen clearly are 45-50µ in long diameter. Sucker spines

are not present. For a description of the rostellum (?) see the discussion following this description.

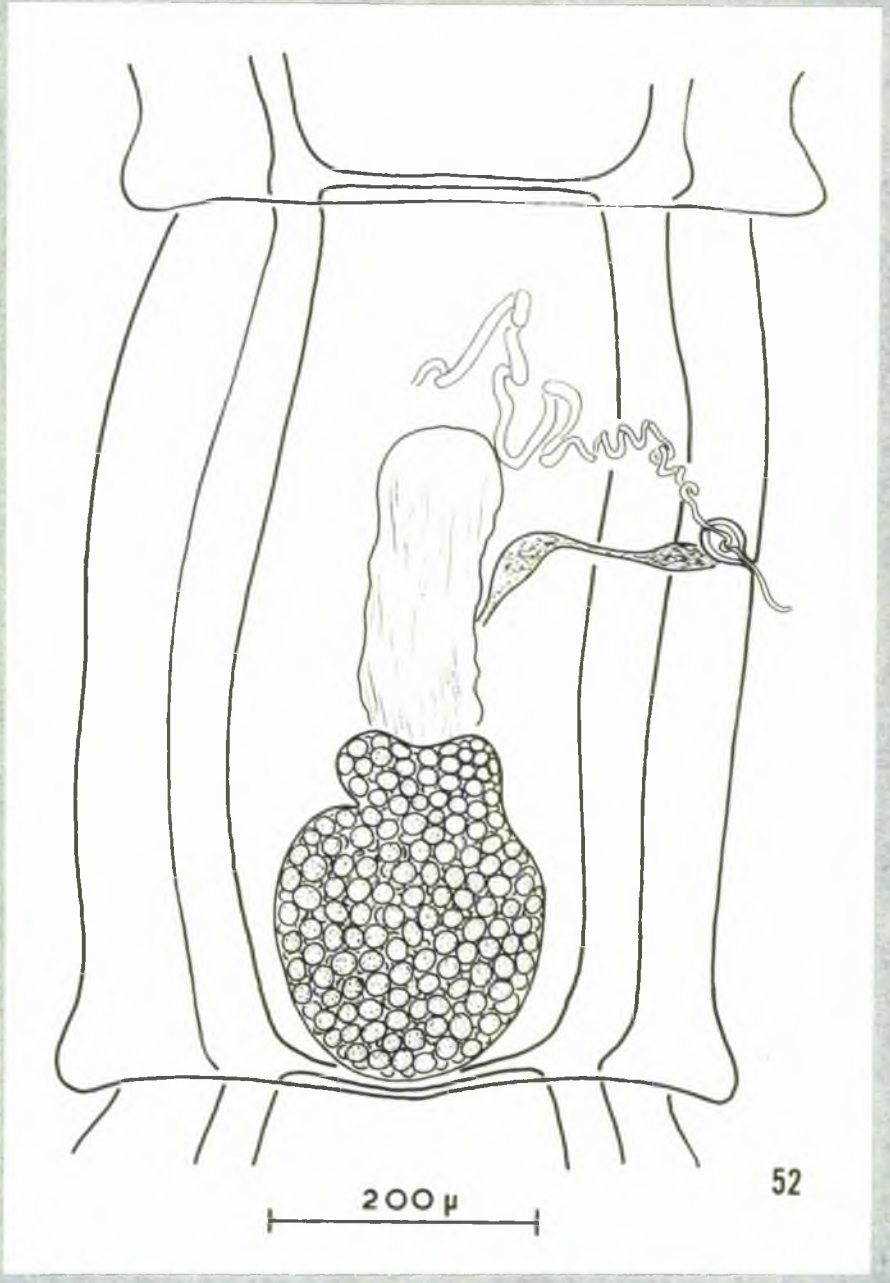


Fig. 52. Ascometra (?) sp. Gravid proglottis.

There are 6-13 testes (Fig. 51) lying mainly posteriorly to the ovary although they may come to lie laterally in some proglottides. The testes measure 37-52μ

by 30-40μ. The cirrus sac, 52-64μ long by 30-50μ in diameter, is situated laterally about one-third the length of the proglottis from the anterior margin. The cirrus, apparently unarmed and short, could be seen in a few proglottides projecting from the cirrus sac. The largest cirrus seen was 35μ long by 4μ in diameter.

The bilobed ovary tends to be slightly displaced towards the aporal side of the proglottis but as it is not lying flat in the majority of proglottides, its full extent is difficult to determine accurately. Immediately behind the isthmus of the ovary is the ovoid vitelline gland which measures 50-75μ by 45-60μ. The vagina, which opens into the genital atrium posteriorly to the opening of the cirrus sac, is relatively short, opening into a small receptaculum seminis which lies almost immediately behind the cirrus sac. The receptaculum seminis measures 35μ by 20μ.

The uterus (Fig. 52) exists as a simple sac-like structure initially which lies in the posterior half of the proglottis within the medulla and not extending beyond the excretory vessels. Just in front of the uterus lies the paruterine organ which gradually surrounds the uterus and rounds it off into an almost spherical structure.

DISCUSSION:

The structure of the scolex is very difficult to ascertain as it is lying in such a position that what at first sight looks like a rostellum may in fact be a third sucker superimposed on a fourth one. In the event that the scolex bears four suckers and no rostellum, it is almost certain that the worm belongs to the genus Ascometra Cholodkowsky, 1913, or perhaps to the genus Orthoskrjabinia Spassky, 1947. If the genital apertures are considered as being unilateral, thereby ignoring the 5% of genital apertures which appear on the "wrong" side, the worm should belong to the genus Ascometra; but if, on the other hand, the genital apertures are simply considered as irregularly alternating, this character would place the worm in Spassky's genus Orthoskrjabinia. In view of the fact that in neither of the two mentioned genera does there exist a worm which agrees sufficiently well with the present worm to warrant identification with it, and in view of the fact that the worms are not in good enough state of preservation to allow a full description, it was thought best that the present material be left unidentified until such a time as more material from Centropus toulou was available.

Notopentorchis collocaliae Burt, 1938

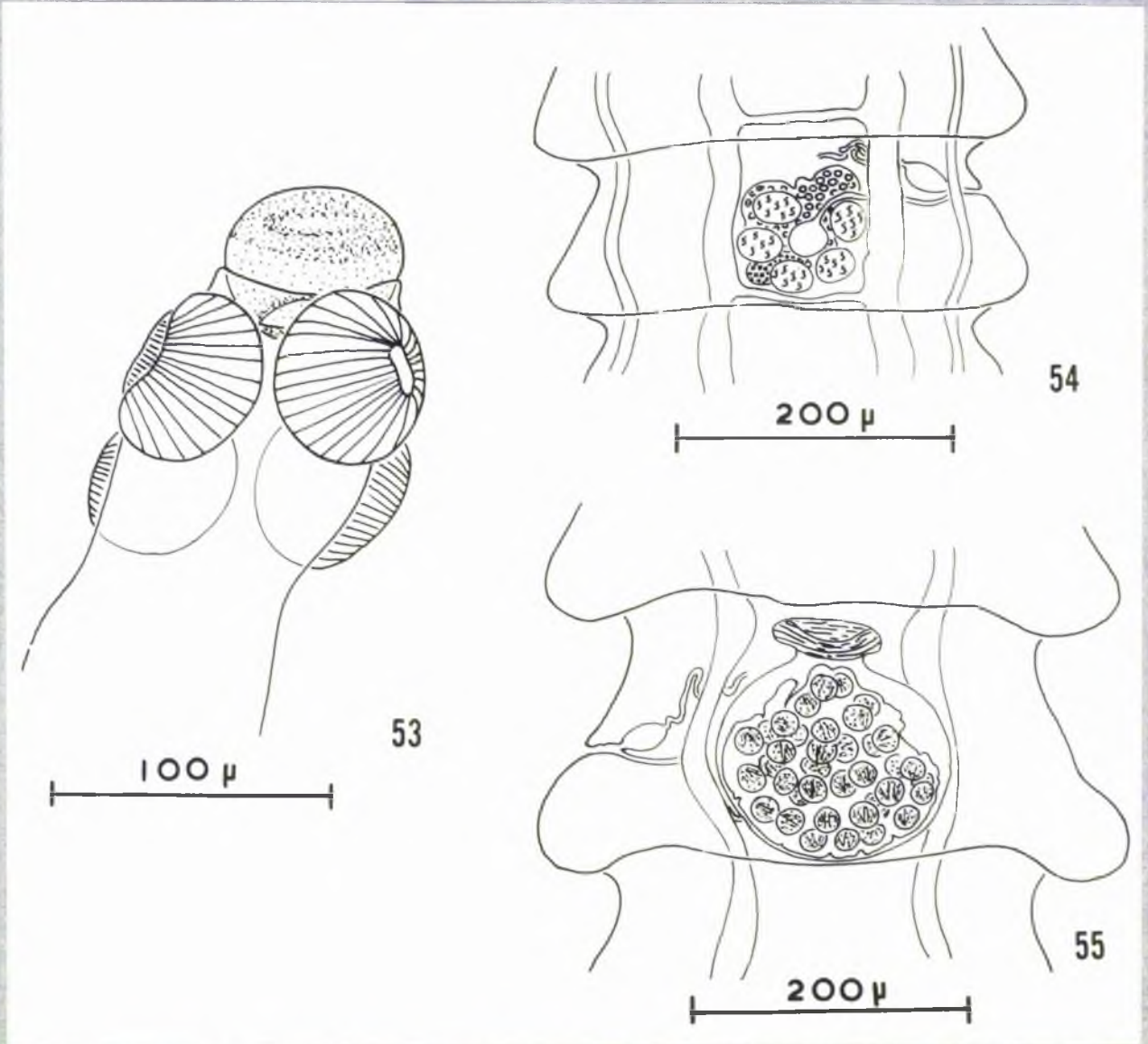
Host: Apus affinis 8784.

The worm is 20 mm long and 0.48 mm in maximum breadth. The proglottides are all, except for some of the most gravid ones, broader than long, the ratio of breadth to length varying from 4:1 to 3:2. The genital apertures are irregularly alternating and the genital ducts pass ventrally to the excretory vessels.

The scolex (Fig. 53) measures 110μ in diameter and has a length, including the length of the rostellum, of 120μ. The suckers are 65-70μ by 50-55μ and are unarmed. The rostellum, 60μ long by 70μ in diameter, is also unarmed but it is presumed that the hooks of the rostellum have been lost.

There are usually five testes (Fig. 54) but an occasional proglottis may contain four or six testes. These are situated posteriorly and laterally to the female genitalia with a tendency also to overlie parts of the ovary and the vitelline gland and they measure 25-30μ by 18-22μ. The cirrus sac is small and most easily seen in gravid proglottides where it measures 30-35μ in length by 16-20μ in diameter.

The ovary, lying in the centre of the proglottis, is large and irregularly lobular, while the vitelline gland which lies posteriorly to the ovary, is also well developed and measures 40-45μ in diameter. Situated above the posterior part of the ovary is the shell gland which has a diameter of 30-35μ. The vagina, which opens into the genital atrium posteriorly to the



Figs 53-55. Notopentorchis collocaliae Burt, 1938. Scolex (Fig. 53), mature proglottis (Fig. 54), and gravid proglottis (Fig. 55).

opening of the cirrus sac, passes ventrally to the excretory vessels and opens into a receptaculum seminis which, in gravid proglottides where it reaches its maximum size, measures 24-33μ by 16-20μ.

The uterus is initially present as a simple sac which rounds off to form a sphere, 120-180μ in diameter (Fig. 55). There are 20-35 eggs per proglottis and the contained oncospheres measure 30-38μ by 24-30μ. The hooks of the oncosphere are of two different sizes: the two lateral pairs are smaller, measuring 13-15μ in length while the medial pair is larger, measuring 16-20μ in length.

DISCUSSION:

The present material agrees very closely with the Ceylon material described by Burt (1938) as Notopentorchis collocaliae for which he created a new species and erected a new genus. Baer (1959), however, transfers to the genus Notopentorchis Burt, Paruterina javanica Hübscher, 1937 and P. bouieni Hübscher, 1937 and places N. collocaliae as a synonym of what is now Notopentorchis javanica (Hübscher, 1937). In Burt's paper, the number of rostellar hooks is not given and Baer estimates the number, from the drawing of the scolex,

to be about 50. Through the kindness of Mr. D.R.R. Burt, I have been able to examine the type material of Notopentorchis collocaliae and find there to be between 30-35 hooks, probably about 32. As there are at least 50 hooks in javanica, according to Baer who re-examined the type material of Hübscher, this would seem to represent a valid differentiating character. This difference, taken with the significant difference in the size of the cirrus sac, undoubtedly separates these two worms and, accordingly, it is proposed here that Notopentorchis collocaliae is a valid species and should not be regarded as a synonym of N. javanica. Singh (1952) describes the species Notopentorchis micropus from Micropus affinis. Although his species differs from collocaliae "in the shape of the hooks, the size of the hooks of the two crowns, size of cirrus pouch, shape of ovary and development of uterus and paruterine organ," it does not differ from Hübscher's species, javanica, with which Singh did not compare it. The apparent difference in number of testes (5 in micropus and 8-10 in javanica) is not a valid difference as re-examination of Hübscher's type material of javanica by Baer indicated that there were never 8-10 testes but only 5. Mokhehle (1951) creates the species Sphaeruterina caffrapi which appears to differ from Notopentorchis

javanica only in the fact that the genital ducts pass dorsally to the excretory vessels instead of ventrally. Baer (1959), however, points out that while the genital ducts are described as passing dorsally to the excretory vessels, they are drawn as passing ventrally. Mokhehle (1951) described a second species of Sphaeruterina, namely S. dikeniensis and again describes the genital ducts as passing dorsally to the excretory vessels but draws them as passing ventrally. Baer assumes that Mokhehle is correct in his drawing but wrong in his description and believes that both worms should be in the genus Notopentorchis, the first one as a synonym of javanica and the second, Sphaeruterina dikeniensis, as a synonym of Notopentorchis vesiculigera (Krabbe, 1869). The accompanying table (Table XII) best illustrates the differences between the four valid species of Notopentorchis.

Species:	vesiculigera Krabbe, 1882	bovieni Hübscher, 1937	javanica Hübscher, 1937		collocaliae Burt, 1938	Borneo material
Description taken from:	Krabbe (1882)	Hübscher (1937)	Hübscher (1937)	Baer (1959)	Burt (1938)	
Strobila (length x max. breadth in mm)	100 x 1.5	78 x 0.918	26.5 x 0.5	25 x 0.59	26 x 0.29	20 x 0.48
Scolex (diameter in µ)	-	408	228	183-260	150	110
Rostellum (diameter in µ)	-	252	135	90-100	82	70
Rostellar hooks (number)	50	70	44-48	50	30-35 (personal count from type material)	hooks lost
Rostellar hooks (length in µ)	37-46 & 20-26	60 & 30	25-28	30-31 & 25-26	27 & 24	
Suckers (diameter in µ)	-	180-228	102	68-75 x 57-75	75	65-70 x 50-55
Testes (number)	-	9-12	8-10	5-6	5	5 (4-6)
Cirrus sac (length x diameter in µ)	-	150-170 x 40	110-120 x 40-50	57-68 x 23	35 x 30	30-35 x 16-20
Oncospheres (diameter in µ)	-	39 x 24	27-30	31-32	28	30-38 x 24-30
Oncosphere hooks (length in µ)	17-19	18	15	-	19	13-15 x 16-20
Host	Hirundo-rustica Cypselus apus	Macropteryx longipennis	Macropteryx longipennis	Apus caffer	Collocalia unicolor	Apus affinis

Table XII

Valid species of Notopentorchis compared with material from Borneo

Gyrocoelia perversa Fuhrmann, 1899

Syn.: Gryocoelia paradoxa (von Linstow, 1906) Fuhrmann, 1908
Gryocoelia milligani Linton, 1927
Gryocoelia pagallae Cable and Myers, 1956

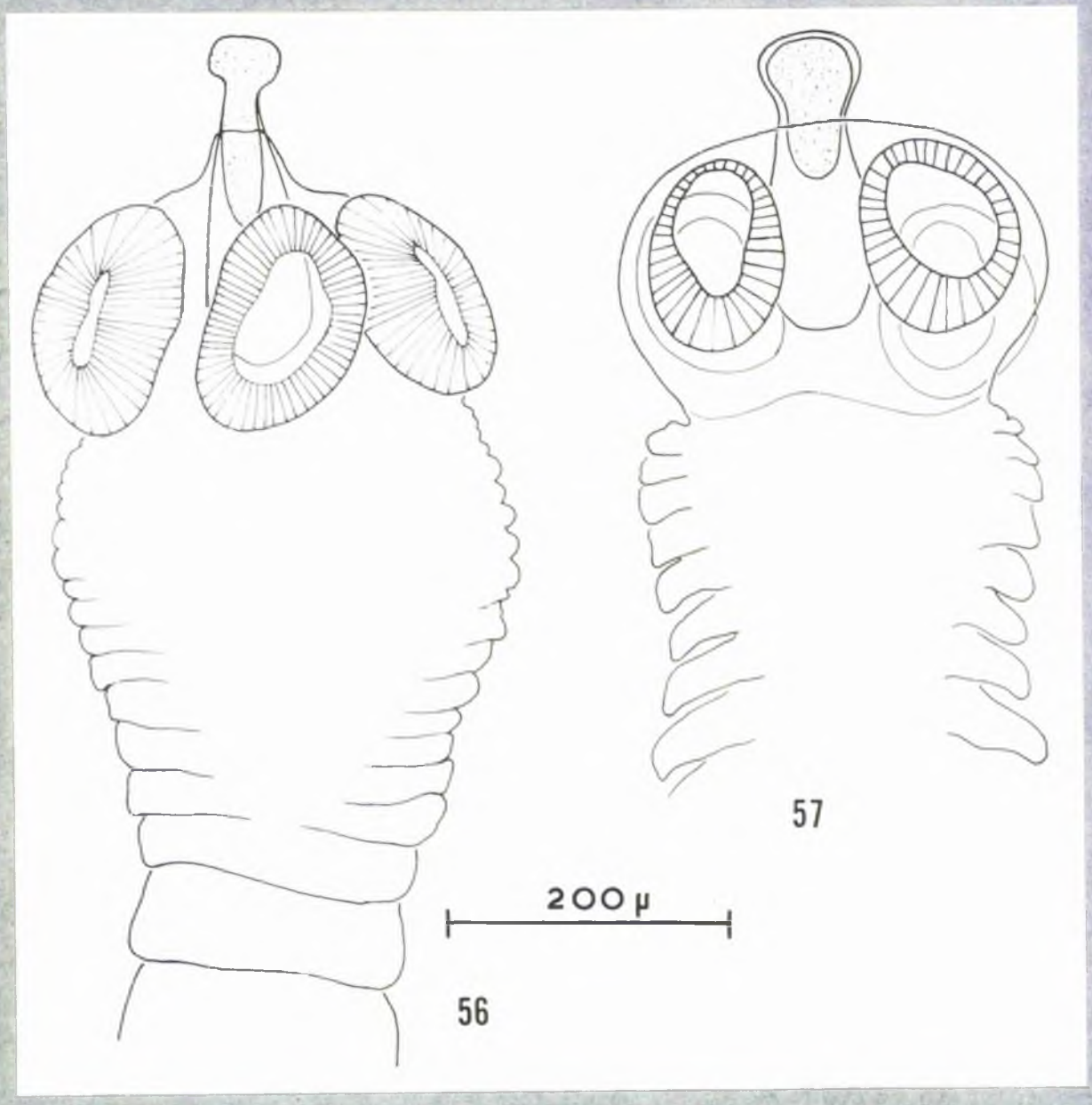
Host: Charadrius leschenaultii 8999;9334.

One full mature 'female' strobila was found in host PJ 8999, and two small, barely mature worms - one male and one 'female' - were found in host 9334.

The scolex (Figs 56 and 57) measures 290-325μ in diameter by 250-280μ in length including the length of the rostellum. The suckers are oval in outline and measure 145-170μ by 100-125μ. No sucker spines were seen. The rostellum measures 150-250μ from the top of the apical cushion to the bottom of the rostellar sac and the diameter of the apical cushion is 50-80μ. No rostellar hooks were seen.

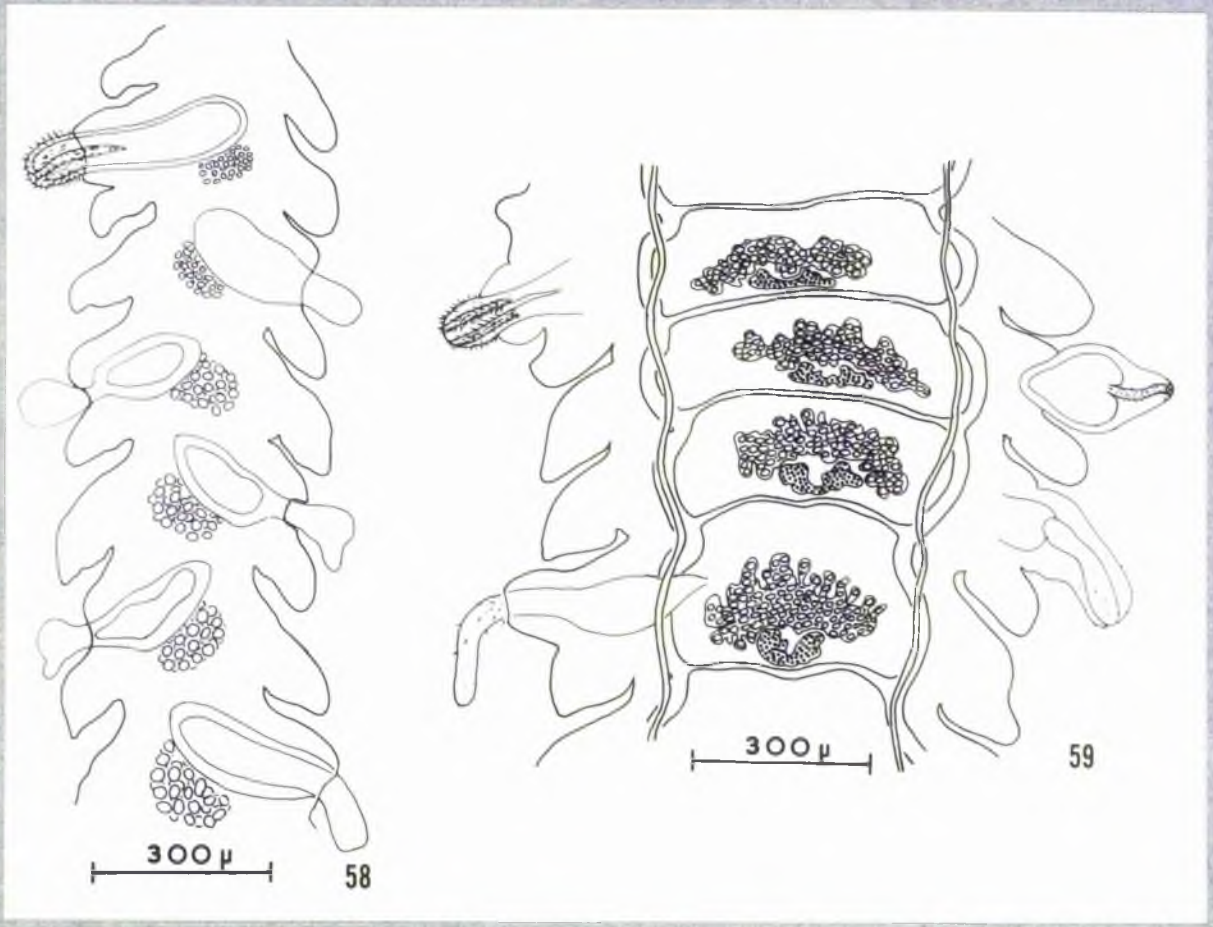
The male strobila (Fig. 58) is not fully mature although in the distal part of the strobila, several cirri can be seen in various stages of extrusion. The length of the strobila is 8 mm and the maximum breadth is 0.9 mm. The testes are present in a compact group about the centre of the proglottis, but are so crowded together that it is not possible to make an accurate count of their

number. There appear to be, however, about 30 testes, the maximum diameter of the most mature testes present being 30-40μ. The cirrus sac measures 240-280μ by 120-130μ and passes between the ventral and the dorsal



Figs 56 and 57. Gyrocoelia perversa Fuhrmann, 1899. Scolex with everted rostellum (Fig. 56) and scolex with retracted rostellum (Fig. 57).

excretory canals. The conical cirrus measures about 250μ in its extended form, has a diameter of 75μ at its base, and a diameter of about 35μ at its apex. During the early part of its extrusion, the long spines



Figs 58 and 59. Gyrocoelia perversa Fuhrmann, 1899. Part of a male strobila (Fig. 58) and part of a 'female' strobila (Fig. 59).

present on the proximal quarter of the cirrus are easily seen and these measure 10-15μ in length when measured from a whole mount.

The smaller 'female' strobila is very similar in external dimensions to the small male, while the larger 'female' (Fig. 59) measures 53 mm long by 2.5 mm in maximum breadth. The ovary is a little over 500μ across by 50-100μ. The elongated vitelline gland measures 230-250μ by 30-45μ. The 'receptaculum seminis' could be seen lying between the ovary and the vitelline gland. In the larger of the two worms, the cirrus sac measures 420-500μ by 110-150μ; while in the smaller worm the cirrus sac is 300-320μ by 120-140μ. The eggs, present only in the larger worm, measure 68-73μ by 35-40μ while the contained oncospheres are 20-30μ in diameter. The hooks of the oncosphere were not examined as squash preparations, but on a whole mount these appeared to be about 8μ long.

The muscular system is very well developed and comprises 100-150 large bundles of longitudinal muscle fibres in two poorly separated layers. Each bundle contains up to 100 individual muscle fibres. The transverse muscles lie between the longitudinal muscle bundles and also round the central medulla. Close to the cuticle lie further individual longitudinal muscle fibres interspersed with large parenchyma cells.

DISCUSSION:

The present material agrees reasonably closely with that described by Baer (1959) as Gyrocoelia perverse Fuhrmann, 1899. Baer places all known species of Gyrocoelia plus Infula burhini Burt, 1939, into two groups. The first of these groups contains Gyrocoelia australiensis Johnston, 1912; G. fausti Tseng-Shen, 1933; G. kiewietti Ortlepp, 1937; Infula burhini Burt, 1939; and Gyrocoelia albaredai Lopez-Neyra, 1952, all of which become synonymous with Gyrocoelia crassa (Fuhrmann, 1900) Baer, 1940. The second group contains Gyrocoelia paradoxa (von Linstow, 1906) Fuhrmann, 1908; G. milligani Linton, 1927; and G. pagollae Cable and Myers, 1956, all of which become synonymous with Gyrocoelia perversa Fuhrmann, 1899.

Although at first sight there appear to be several differences between the two groups, few of these are significant. Perhaps the most striking differences are found in the size of cirrus sac, the number of testes and the diameter of the scolex. In perversa, the cirrus sac tends to be smaller and measures up to about 400μ by 137-146μ while in crassa, the length of the cirrus sac reaches up to 650μ and its diameter is 195-260μ. in

perversa there tend to be fewer testes, numbering 20-30, whereas in crassa the number ranges from 30 to 50 per segment. Although the upper number of testes in perversa coincides with the lower number of testes in crassa, the average number of testes found in any one worm can usually place it unambiguously into one or other of the two species. Finally, in perversa the diameter of the scolex is about 320μ whereas in crassa it is considerably greater, measuring 411-457μ. It is not unlikely that there exists a graded series of forms and that one worm may exhibit features in common with both species. For instance, the present material possesses about 30 testes and thereby lies about half-way between perversa and crassa. Another feature which would place it in this anomalous position is the size of the cirrus sac, particularly that of the large 'female' strobila which, although far from reaching the upper limit of size of cirrus sac found in crassa, is nevertheless substantially bigger than the cirrus sac described for perversa. The size of the scolex, the diameters of the suckers and, to a certain extent, the overall size of the worm all indicate that it is perversa.

Owing to the fact that the present material possesses no rostellar hooks, it was first thought that

the worms belonged to the genus Infula Burt, 1939. The two main features of difference between Infula and Gyrocoelia are that Infula is dioecious and there are no rostellar hooks whereas in Gyrocoelia there are rostellar hooks, and initially the worm was considered by most as a normal hermaphrodite worm. Early workers described Gyrocoelia as possessing testes and ovaries in the same strobila and, furthermore, in some cases actually figured them together in the same proglottis. However, Baer (1959), by re-examining much of the type material, has been able to show that testes do not occur in the same strobilae as ovaries. Furthermore, Baer examined the type material of Infula burhini Burt, 1939 but was unable to substantiate Burt's hypothesis that the structure corresponding to the cirrus sac in the male, functioned as a vagina in the female, particularly as he could not find sperm in the proximal portion of the 'vagina' where it should undoubtedly be in the event of that structure functioning as a vagina. In view of this, and in view of the fact that it is generally recognised that the rostellar hooks of Gyrocoelia are highly caducous, Baer felt justified in treating Infula as a synonym of Gyrocoelia and making Infula burhini a a synonym of Gyrocoelia crassa. The fact that sperm

are found in the 'receptaculum seminis' is explained by Baer with the hypothesis that the female strobilae are cryptohermaphrodite and that sperm are produced by testicular tissue which is present in the walls of the 'receptaculum seminis'.

Even although Baer considers that Infula should belong to the genus Gyrocoelia, on the grounds stated, it is by no means improbable that Infula may well be a valid genus, principally on the basis of its lacking rostellar hooks. Recognising that rostellar hooks may easily be lost in fixing and preserving worms, towards the end of his discussion on Infula burhini, Burt (1939) states the following:

"The worms described in this paper were obtained in the field from birds shot for their parasites. They were fixed in Bouin's fluid on the spot, hence their state of preservation and fixation is good. Cestodes collected under these conditions and before fixation allowed to detach themselves from the wall of the gut by placing the opened gut in water, very rarely lose their rostellar hooks. Thus one has little hesitation in accepting the absence of hooks in the six specimens as being a diagnostic character. Infula is most nearly allied to Shipleya and

Gyrocoelia, and is distinguished from these, apart from its dioecious character, by the character of the rostellum. The rostellum is absent in Shipleya, a fact which was ascertained by Fuhrmann from sections of the scolex; it is present and characteristically armed in Gyrocoelia; and present but unarmed in Infula."

Coil (1955) describes a new species of Infula, namely I. macrophallus, and in a later paper (Coil, 1963) he discusses the validity of the genera Gyrocoelia and Infula. His conclusions, which are based on careful examination of worms from freshly killed hosts, indicate that not only is the scolex of Infula consistently unarmed, but that there are highly significant differences in the egg membranes of members of the two genera. These differences are elegantly shown by using various histochemical techniques such as those used by Ogren (1959 and 1961).

Burt has recently made a large collection of worms from wading birds in North America and it is hoped that examination of this new, carefully fixed and preserved material, will throw further light on the genus Infula particularly in relation to the cryptotestes suggested by Baer.

From the same host species, namely Charadrius leschenaultii, there were found what appear to be three different worms all of which, however, almost certainly belong to one or other of the families Acoleidae, Progynotaeniidae, and Dioecocestidae. Brief descriptions of them are given here due to their probable relationship with Gyrocoelia and they are described simply under the headings of Species 1, Species 2 and Species 3.

Species 1

This is represented by three small worms in poor state of preservation which probably belong to the genus Progynotaenia, or perhaps Andrepigynotaenia. The longest worm measures 6 mm long by 0.7 mm in maximum breadth. The genital apertures are irregularly alternating.

The scolex has a diameter of 150μ and is 150μ long, the length being taken to include the length of the rostellar sac. The four suckers are approximately 75μ in diameter but appear to be degenerating. No sucker spines were seen. The rostellum measures about 60μ long, the rostellar sac about 90μ long, and the apical cushion has a diameter of 52μ. No rostellar hooks were

seen, but there appear to be 11 or 12 scars present on the rostellum which may well mark the sites of hooks that have been lost.

Although the worm is not in a very good state of preservation there appear to be about 7 testes, the range possibly being 6-10, which have a diameter of 30-40μ. These were best seen lying alongside the developing uterus and were scarcely visible in any but two proglottides. The cirrus sac is 150-200μ long by 70-80μ and is not fully developed until the uterus is well formed and the ovary and vitelline gland have both disintegrated. There does not appear to be either an external nor an internal seminal vesicle, the vas deferens lying slightly twisted and swollen outside the cirrus sac and the ductus ejaculatorius lying in a few loops in the proximal portion of the cirrus sac.

The ovary measures about 125μ by 90μ just before it starts to enlarge with what appear to be fertilized eggs. The vitelline gland, situated ventrally and posteriorly to the ovary, is more or less spherical with a diameter of about 70μ. The receptaculum seminis is large, measuring up to 230μ by 110μ, and can be seen in several proglottides as a swollen sac full of sperm.

There are no fully-gravid proglottides but in the more mature proglottides, the uterus can be seen as a large sac-like structure almost completely filling the medulla of the proglottis.

Species 2

This is represented by one worm, 9 mm long and 0.52 mm in maximum breadth. The proglottides tend to be triangular in shape, longer than broad initially but becoming slightly broader than long. The genital apertures are regularly alternating.

The scolex has a diameter of 175μ across the suckers and a length of 180μ including the length of the rostellum. The four suckers are 85-95μ in diameter and appear to be unarmed. The rostellum also apparently unarmed, measures 144μ from its tip to the bottom of the rostellar sac.

The strobila appears to comprise solely male proglottides, but owing, perhaps, to the poor state of preservation, no testes were seen. The cirrus sac is large and in many of the more distal proglottides, could be seen projecting well beyond the lateral margin of the strobila. It measures 315-350μ long by 110-130μ in diameter and in early proglottides can be seen to contain

a large, profusely spined, cirrus. In the later proglottides, when the cirrus, which reaches over 300μ in length, has been extruded, the spines are no longer visible and presumably have been lost.

No other anatomical features could be made out.

Species 3

This species is represented by a single worm with a scolex which bore three hooks. The material is in an advanced state of decomposition and the only data of any significance is the shape and size of the hooks.

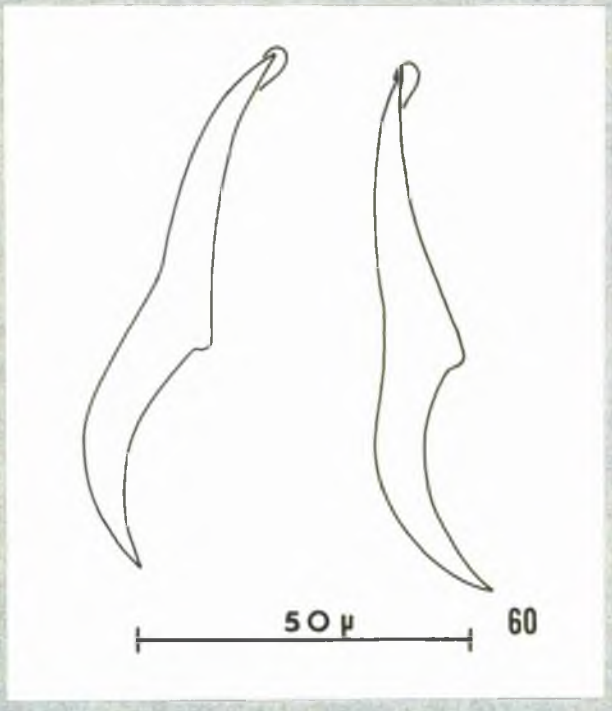


Fig. 60. Species 3. Rostellar hooks.

Measured under oil immersion in a squash preparation, the hooks (Fig. 60) are 85μ, 86μ and 89μ long, although one, the largest, is slightly twisted.

DISCUSSION:

Although Webster (1951) gives a useful table of species in the genera Progynotaenia and Proterogynotaenia and Sandeman (1959) gives a more recent review of the genus Proterogynotaenia, none of the above three species could be identified. There is only one worm described in the genus Andrepigynotaenia Davies and Rees, 1947, and that has many more testes (58-70) than is apparent in any of the above. It may be that one or more of the above three represents a new species but as the material is neither in good condition nor complete, the erection of any new species is hardly justified.

PART II

INVESTIGATION INTO THE PROBLEM OF HOST SPECIFICTY BY MEANS OF EXPERIMENTAL INFESTATION

PREFACE TO PART II

The fact that the environment provided by a host can affect the morphological development of a cestode parasite within it is well substantiated by various workers (Beck, 1951, 1952; Read, 1959; Read and Simmons, 1963; Smyth, 1947, 1963 and Schiller, 1959) and the fact that the special requirements of each species of cestode were met only in certain species of hosts was recognized as far back as 1869 by Krabbe who first envisaged the concept of host specificity in cestodes. This concept has been amply confirmed by Fuhrmann (1932) in birds and later by Joyeux and Baer (1936) in mammals. Most of the investigations regarding the effects produced on tapeworms by environmental changes have been carried out by altering the nature of the food ingested by the host or, in a few experiments, by altering the hormonal balance of the host. Such effects as were produced and recorded were of an obvious nature where growth stopped, or abnormal egg production ensued, and this type of effect is more or less in keeping with the drastic nature of the experiments carried out. The slight differences which might naturally occur in the environment of a tapeworm provided by two different

species of host, however, have not been investigated and any such investigation must rely on thorough morphological observation coupled with a knowledge of the normal range of morphological variation found in a cestode from any single species of host. The aim of the work in this part of the thesis was to determine whether differences present in the environments provided by different hosts resulted in morphological differences in the same species of cestode. Furthermore, it was intended to investigate whether differences in cestode morphology were constant and specific for different hosts. In the event of morphological differences being manifest, it was intended that they be investigated carefully with a view to establishing whether they might constitute characters that had hitherto been used to separate a single species of cestode into two separate species.

The approach employed was to infest, artificially, different species of hosts with larval cestodes from a single source and then to compare the fully developed adult worms which were to be recovered from the infested hosts following post-mortem examination. In each case, a variety of different host species were to be used, one of these species representing the normal host species for the cestode concerned. Thus, any adult worms

recovered could be compared directly with control worms from a normal host. Various cestodes were considered for investigation, including Raillietina, Dilepis, Taenia, Ophryocotyle, Paricterotaenia, and Diplocotyle and in each case a search was carried out for larval material. The numbers of potential intermediate hosts examined for each of the cestodes listed is given in Appendix I along with the number found to be infested. Where larval material was found, it was used in experimental infestations but in all cases except Diplocotyle normal hosts for the cestode species used were not available or could not be kept in captivity. The fact that no adult tapeworms were recovered from the experimental infestations, except in the case of Diplocotyle, further substantiates the concept of host specificity as the only experimental hosts used were animals in which the cestode species under investigation have not been found. The experimental infestations carried out using Ophryocotyle and Paricterotaenia are summarized in Appendix II. The studies carried out in relation to Diplocotyle yielded the only positive results from experimental infestations tried and the work on this species is described as follows.

Diplocotyle

Introduction

This cestode was found in the St. Andrews area by I. M. Sandeman in 1961 (Sandeman, 1962) but had apparently disappeared from the area following some severe storms. It was accidentally rediscovered during the present work while collecting Marinogammarus to feed to ~~the~~ a captured turnstone. Although the incidence of infestation was low (approximately 0.02%) it was possible to collect over 20 infested Marinogammarus owing to the relative ease of differentiating between infested and non-infested individuals. The main criterion used in differentiating between infested and non-infested individuals was the colour; those which were non-infested showed the normal dark, gray/green appearance, whereas those with tapeworms appeared much paler, being even light gray in some instances. The latter were kept alive and used in various ways to be described later.

One of the most perplexing features concerning the infestations, however, was the apparent total absence of young larval cestodes in the large numbers of Marinogammarus examined. Over 2,000 individuals were examined specifically for the possible presence of young larval stages but none was found. This lack of young larval

stages could suggest that the life cycle is seasonal or that a prior intermediate host exists. According to Dr. U. Paim (personal communication) gammarids are mainly carnivorous but also feed on diatomaceous and algal material. This means that they could either pick up the eggs, or that they could ingest a young larval form which might be present in another host. Accordingly, various possible organisms were examined, particularly small annelids which were found in the same ecological niche as Marinogammarus, but in no instance was any young larval stage found. Evidence that the life cycle may be seasonal comes from the fact that Sandeman found worms at the same stage of development at the same time of year. If such seasonal variation did exist, then the apparent disappearance of infested hosts could well be accounted for in terms of a different stage in the life cycle. The life cycle of the primary host, Salmo, Pleuronectes, etc., may also play an important part in the appearance and disappearance of infested Marinogammarus at different times of the year.

The cestodes found infesting Marinogammarus are almost unique in the respect that these larval forms have apparently reached sexual maturity in an invertebrate host in so far as they possess large numbers of

eggs. The only other worms, so far recorded, which also become gravid in the intermediate host belong to the genus Archigetes. Work done by Wisniewski (1928, 1930), Calentine (1964), and Kennedy (1965) suggests that the adult worm of Archigetes, as present in Limnodrilus or other aquatic oligochaete worms, represents a neotenic procercoid and that a simple life cycle exists in which the liberated eggs are eaten by the tubificid host where they develop directly to sexual maturity in the coelome. Kennedy (1965) shows the relationship of Archigetes to other genera in the family Caryophyllaeidae and arranges the various genera to show that a series exists in the attainment of neoteny within the family. All the fully neotenic forms are included in the genus Archigetes but other genera such as Caryophyllaeus and Biacetabulum approach the neotenic condition in so far as development of the genitalia may take place in the invertebrate host. In neither of the latter two genera, however, does any worm become gravid until it reaches the definitive host, a fish. Other genera such as Monobothrium and Glaridacris also show development of the genitalia in the invertebrate host but the life cycles of these two genera have not been

fully investigated. Future work on the life cycle of Diplocotyle is intended and it will be interesting to see how this worm, along with other genera in the family Cyathocephalidae, compares with those genera in the family Caryophyllaeidae.

The taxonomic position of Diplocotyle and Bothrimonus, a genus frequently confused with Diplocotyle, is extremely uncertain even as to whether the family Cyathocephalidae should be included, along with the Caryophyllaeidae, in the order Pseudophyllidea. Joyeux and Baer (1961) favour the view of Nybelin (1922) who erected the family Cyathocephalidae to contain Diplocotyle among other genera and who considered them as belonging to the order Pseudophyllidea. Wardle and McLeod (1952), on the other hand, place Diplocotyle, Bothrimonus, and Didymobothrium in the family Diplocotylidae and include this family along with the families Spathebothriidae and Cyathocephalidae in the order Spathebothridea. They erect this new order to separate the forms listed above from those included in the Pseudophyllidea on the basis that there is no evidence that the holdfast of the above forms has been derived from bothria. The relationship and possibly synonymy of the genera Diplocotyle and

Bothrimonus are discussed fully in Appendix III from which it appears that many of the more recent workers prefer the view of Wardle (1932) and Nybelin (1922) that both of these genera are valid and that the genus Diplocotyle should not become a synonym of Bothrimonus.

The evidence put forward by Schneider (1902) and also by Cooper (1918), however, suggests that Diplocotyle should in fact be synonymous with Bothrimonus and this view would tend to be confirmed by observations made of the present material while it was alive. The tremendous capacity for drastic changes in shape of the scolex and the manipulation of the suckers leaves little doubt that depending upon the state of contraction, the scolex could appear to have a single, or a double, anterior sucker. In view of the present taxonomic chaos, however, any identification of the present material can only be tentative, so despite the evidence which suggests that only the genus Bothrimonus be considered as valid for the group of worms mentioned above, it may be better, meanwhile, to retain both generic names until such time as the type material, and fresh material from different hosts, can be examined in the light of all the previous literature.

Wardle (1932) considers that more light could be shed on the problem if new material from sturgeon in North America were examined, but so far all the sturgeon from New Brunswick which have been examined, have not contained any cestodes at all. Examination of Pseudopleuronectes americanus for possible infestation with Diplocotyle is currently being carried out and it is intended that the whole problem of taxonomy of this group of worms and also the problem relating to its full life cycle be tackled in the near future. Until then, the present material will be tentatively identified as Diplocotyle nylandica (Schneider, 1902) Nybelin, 1922. One of the main reasons for allocating these worms to the species nylandica lies in the fact that Nybelin, in his redescription of this species, states that the testes are either single, shrunken, or missing. In the species olrikii, however, he indicates that the testes are well developed. Whether this is a valid differentiating feature is highly doubtful as it seems more than likely that the degree of development of the testes could far better be explained in terms of age of the worm. However, it is an established fact that the present worms from Marinogammarus do not possess any visible testes, visible either with the light microscope or with the electron

microscope, and accordingly in this respect, the present material agrees well with the species nylandica as described by Nybelin. The lack of testes in the present material will be discussed later but it can be pointed out here that all the worms examined were collected at approximately the same time of year, were all at the same stage of development, and were, therefore, possibly of the same age. A recent paper by Stark (1965) indicates that a species of Diplocotyle is also found in Gammarus zaddachi zaddachi Spooner in the river Esk in Yorkshire and it is particularly interesting to note that examination of large numbers of gammarids throughout the years 1959-1962 revealed the presence of Diplocotyle plerocercoids during December to April only. Furthermore, Stark was unable to find any procercoids at all despite the fact he was looking for them. The Gammarus infested with plerocercoids disappear abruptly in April and Stark correlates this with the seaward migration of salmon smolts at this time of year and indicates that as infested Gammarus, harbouring large parasites, tend to float upwards and actually become stuck conspicuously to the surface of the water, being too weak to break free of the surface tension, this probably renders them easy victims to such predators as

salmon. While such an explanation might well hold good for river and estuarine gammarids it does not seem as likely for marine forms. However, if those gammarids with large parasites do tend to float, they would be more likely, during a storm, either to be swept to sea or thrown up on the shore than would those individuals which could maintain their position under rocks and stones in the intertidal zone. This could, therefore, explain the disappearance of infested Marinogammarus from the St. Andrews area following storms in March and April.

The first collection of Marinogammarus containing Diplocotyle was made personally in February, 1964 and the later two collections made by Mr. D. R. R. Burt at about the same time of year in 1965 and 1966. I should here like to express my thanks to my supervisor for making these other collections for me so that I had fresh material which could be examined particularly for the presence of testes and which could generally be compared with worms of the previous collection. I should also like to express my thanks here to Mr. R. W. Ingle of the British Museum (Natural History) who kindly identified the specimens of Marinogammarus as M. pirloti Sexton and Spooner. The gammarids in which Sandeman found Diplocotyle, which came from the same area, were identified by him

as Marinogammarus finmarchicus in a personal communication to Stark (1965). Should both identifications be correct, it would appear that Diplocotyle from the St. Andrews area is not as host specific as the worms recorded by Stark in the Esk as these latter parasitized only one out of seven species of gammarids present. The six species in which Diplocotyle did not develop are identified by Stark as: "Gammarus pulex L., G. duobeni Lillj., G. locusta, G. zaddachi salinus Spooner, Marinogammarus marinus Leach, and M. obtusatsus."

Adult worms of Diplocotyle have been shown to infest several different fish hosts including both flat-fish and salmonids. Each of these general types of fish have different habits, most of the flat-fish being essentially marine throughout their life, whereas a greater part of the life of many salmonids is carried out in fresh water. The flounder, Pleuronectes flesus L. is listed by Wardle and McLeod (1952) as a host of Bothrimonus cohaerens Linstow, 1903 and also as a host of B. nylandicus Schneider, 1902, synonym of Diplocotyle olrikii Krabbe, 1874 and it is interesting to note that this fish is commonly found both in salt water, river estuaries, and fresh water and in this respect is not

unlike salmonids. Marinogammarus is similarly found in all three habitats and all the gammarids collected during the present work were under stones in the bed of a trickle of fresh water so that when the tide was out they were in fresh water but when the tide came in they were in salt water.

As both trout and plaice were available, and as it seemed reasonable to suppose that their metabolism might be sufficiently different to provide internal parasites with different environments, these fish were used in experimental infestations with plerocercoids of Diplocotyle.

Experimental Infestation of Fish

Experiments and results

Following initial infestation of two trout and two plaice each with a single plerocercoid, a week was allowed to elapse before post-mortem examination of the infested fish was carried out. No adult worms were recovered from either the trout or the plaice. This was considered possibly to be a reflection on the infestation technique which involved introducing the larval worms into the oesophagus of the fish with an eye-dropper.

Four more trout and four more plaice were infested, each with a single worm. This second experimental infestation was carried out using a hypodermic syringe attached to a thin piece of plastic tubing, the diameter of which was just large enough to take the larval worm. The tube was then introduced into the stomach of each fish and a single worm injected. The fish were observed for 30 minutes in case the worms were ejected but in no instance was this observed.

Twenty-four hours later, one trout and one plaice were examined and in both fish the worm was recovered. Two days after the initial infestation a second

trout and a second plaice were dissected and although the worm was recovered from the plaice, the worm initially introduced into the trout was not found. Post-mortem examination of the remaining four fishes was carried out four days after the infestation but no further worms were recovered. Worms which were recovered were active when found but the three were only lightly attached to the intestinal wall.

It was hoped that a third run could be carried out, but no more infested Marinogammarus could be found. This is in keeping with what Sandeman found regarding the disappearance of infested forms three years previously.

Discussion

As very little work has so far been done on the ultrastructure of cestodes, and as it seemed quite possible that there may be present some differences between the material recovered from trout and that recovered from plaice which would not be apparent using only a light microscope, it was considered that it would be worthwhile to fix part of each worm recovered for future examination with an electron microscope. Accordingly from each worm recovered, a small section was

cut out and this cut down further into cubes of about 1 mm across. These were then fixed in Palade's fixative and later embedded in Araldite. Sections were cut at about 600 Å and were double stained using uranyl acetate and lead citrate. These were examined with a Siemen's Elmiskop I electron microscope and representative areas photographed. I should here like to express my sincere thanks to Dr. H. C. MacGregor and to Mr. J. B. Mackie for the time spent and help given relating to this phase of the work.

The rest of each worm which was recovered following infestation of the fish was fixed in Bouin-Hollande fixative; part of each was embedded in paraffin wax (melting point 54°C), and the rest mounted whole. Both transverse and horizontal sections were cut from the embedded material at various thicknesses and these were stained either with Ehrlich's haematoxylin and eosin, or with Mallory's triple stain. Whole mounts were previously stained in one or other of the following: Ehrlich's haematoxylin, Delafield's haematoxylin, hydrochloric acid carmine, or acetic acid alum carmine.

Several worms, dissected out of infested Marinogammarus, were treated in the same way as the worms

recovered from the experimentally infested fish and these were then compared at the morphological level, using light microscopy, and also at the subcellular level using electron microscopy. Apart from the development of testes, no differences were apparent, using light microscopy, between the worms found in Marinogammarus and those recovered from either trout or plaice and accordingly the description that follows applies equally well to any of the present material. There is, however, a significant difference between the present material and material which was kindly lent by Mr. S. Prudhoe of the British Museum from Salvelinus alpinus collected in Greenland. This latter material was identified by Mr. Prudhoe as D. olrikii before being loaned, and the differences present will be discussed following the description of the present material from Marinogammarus.

As can be seen from the discussion of the fine structure of this worm, following the morphological description, there is a difference between the larval forms found in Marinogammarus and the forms recovered from both fish hosts but no significant difference could be found between the worms recovered from plaice and the worm recovered from trout.

Investigation of Life Cycle

Experiments and results

As the life cycle of this worm was not known, and as all the worms recovered from M. pirloti were gravid, containing large numbers of eggs, various attempts were made to infest different invertebrate hosts using the eggs of these precocious larvae. Initial examination of the eggs from the plerocercoids showed that although the eggs were operculate and had a tanned shell, embryonation did not appear to be complete. It was assumed, however, that the eggs were viable and that embryonation would take place sooner or later while the eggs were in sea water. In view of the strong possibility that the whole life cycle could be completed within a single host, such as had been found for Archigetes, several attempts to infest gammarids of different ages and different sexes were also made. Some of these experiments are outlined below:

Experiment I.

Three male M. pirloti, all infested with Diplocotyle, were kept in a small glass container (2" diam. by 2" high) with four uninfested individuals of which two were female and two were male. All three infested males were seen to contain gravid worms.

Ten days later, of the seven M. pirloti which had been placed in the container, two were found to have died, one of which had disintegrated. Of the four uninfested individuals, one (female) was moribund, and the other three were still alive. The last infested Marinogammarus was removed and the worm dissected out and fixed for microscopic examination. The moribund uninfested Marinogammarus was also removed and examined carefully for any possible early larval stage. None was found. Examination of the water showed the presence of a high concentration of cestode eggs which must have come from the disintegration of the infested individual with its contained parasite.

Thirty days after the start of this experiment, the remaining three Marinogammarus, all of which were uninfested initially, were removed and examined thoroughly for possible larval stages. None was found.

Experiment II.

Six uninfested Marinogammarus, three male and three female, were placed in a container, as described in Experiment I, with a gravid worm which had been dissected out of another, infested, Marinogammarus.

One day later, examination of the water showed the presence of large numbers of eggs but the worm was still intact.

Two days after the start of the experiment, the worm was found to be disintegrating and even more eggs were present in the water. The disintegrating worm was removed but the eggs and uninfested Marinogammarus were left together.

Fourteen days after the start of the experiment, all six Marinogammarus were still alive but none showed any external sign of contained larvae.

Thirty-five days after the start of the experiment, only four of the initial six uninfested Marinogammarus were still alive. These were removed along with the two dead individuals and all six were dissected carefully and examined thoroughly for possible larval stages. None was found.

Experiment III.

Three small polychaete worms, probably belonging to the genus Nereis, were placed in a container with a gravid Diplocotyle that had been cut into pieces.

After 10 days, one worm was removed and examined carefully for possible larval stages. None was found.

After a further 10 days, a second worm was removed and examined for possible larval stages. None was found.

Twenty-five days after the start of the experiment, the third worm was found dead. It was examined carefully but no larval stages were found.

Several other attempts to infest both gammarids and various other invertebrates with a possible first larval stage (procercoid), similar to the attempts described above, also met with no success. Other invertebrates used were: Harmathoe, Polynoe, Phyllodoce, Littorina, Mytilus, Nucella, Trochus(?), Balanus, Leander(?), Lineus(?), Tubulanus(?).

Discussion

Most Pseudophyllidea have two larval stages in their life cycle. The first larval stage, the procercoid, is frequently found in a crustacean while the second larval stage, the plerocercoid, commonly develops in a fish. If the worms found in Marinogammarus are

procercoids which, like those of Archigetes, have developed precociously as neotenic larvae, then provided the eggs are viable, it should be possible to infest other Marinogammarus by feeding them eggs. All attempts to do so, however, failed and this can perhaps be accounted for in a number of ways: (1) the worms are not neotenic procercoids which have reached the plerocercoid condition by direct development from the egg in a single host, but possibly are true plerocercoids which can only develop from a procercoid in some prior intermediate host; (2) the eggs are not viable; (3) the time of development is so long that the experiments attempted were terminated too soon, in most cases with the experimental animals dying within a month or two. Each of these possibilities are considered as follows: (1) In view of the fact that a crustacean such as a gammarid normally acts as the first intermediate host in the life cycle of those Pseudophyllidea so far investigated, and as none of the other invertebrate hosts investigated in the present work could be infested with the procercoid stage, it is here proposed that the worms recovered from Marinogammarus are probably forms which have developed directly following an initial infestation

with eggs. The present forms are thus considered as plerocercoids which have developed from the egg through the procercoid stage within the same host rather than a normal plerocercoid which has developed within the second intermediate host following ingestion by that second intermediate host of the procercoid within a first intermediate host. (2) The viability of the eggs is questioned in view of the apparent lack of testes in the worms from M. pirloti and in view of the fact that these did not become visible until the worms had reached the definitive fish host. However, although it seems unlikely that the eggs had been fertilized, it is possible that the testes had been present in an earlier stage than that found and had since disappeared and that sperm produced may have fertilized the eggs which were present in the uterus. It is also considered possible that such eggs produced by the neotenic plerocercoids might develop parthenogenetically.

However, eggs which were kept at 38 F in sea water were examined every second day over a period of five weeks and during this time, no development of an oncosphere was observed. The contents of the eggs were seen to have shrunk and the operculum in many cases was

observed slightly separated from the rest of the shell by the end of the five-week period but neither an embryo, nor an embryophore, nor oncosphere hooks were seen in any of the eggs examined.

In the case of Archigetes limnodrili (Yamaguti, 1934), embryonation takes around 20 days at 14°C (Kennedy, 1965) and in the case of Schistocephalus solidus (Creplin, 1829), embryonation takes about three weeks (Callot and Desportes, 1934). Although it is possible that the eggs in the present case might have developed had they been left longer or had they been kept at a higher temperature, the fact that no development was observed over a five-week period strongly suggests that they were not viable. (3) In view of a possible lengthy period of embryonation (over five weeks) if the eggs are in fact viable, and in view of the length of time it would probably take for a hexacanth embryo to develop into a recognizable procercoid (about 30 days in Archigetes limnodrili according to Kennedy, 1965) it is clear that none of the present experiments was continued for a sufficient period of time for any possible infestation to become apparent.

Of these, and other possible explanations, the most likely is that the eggs have not been fertilized as the testes are not yet visible in the plerocercoids, although traces can be seen in the worms recovered from the experimentally infested fish, and that the eggs, accordingly, are not viable.

Diplocotyle nylandica (Schneider, 1902) Nybelin, 1922.

Morphology:

The length of the specimens varies from 50 to 110 mm and their maximum breadth is 0.6 to 1.8 mm. The scolex bears two, more or less fused, suckers which are separated by a ridge of tissue during one stage of contraction but which are joined during another stage of contraction. The overall breadth of the scolex is 560-720μ; its length is 320-400μ; and the diameter of the suckers is 400-480μ. The scolex is well separated from the neck by a sharp indentation while the neck itself is extremely short, the genitalia starting almost immediately behind the scolex. The strobila is not segmented externally but the genitalia occur in more or less separated groups at regular intervals throughout the length of the worm. All groups of genitalia appear to be at the same stage of development in any one worm, including even the first group which arises almost immediately behind the scolex. The distance between adjacent cirrus sacs varies slightly but is usually between 700 and 800μ.

The cirrus sac (Plate 1) measures up to 240μ long by about 150μ in diameter and carries an unarmed

cirrus. The ductus ejaculatorius (Plate 2), which leads through the cirrus sac into the cirrus, is surrounded by small gland cells and has a thick, plicated muscular wall. There is present a large, coiled vas deferens which is situated dorsally to the ventral cirrus sac and which does not appear to contain any sperm in those worms examined from Marinogammarus or in those worms recovered from the experimentally infested plaice and trout. No testes were seen in those worms examined from Marinogammarus, but in the worms recovered from the plaice and to a certain extent also the worm from trout, rudimentary testes (Plate 3) could be seen developing in the lateral medullary regions, immediately inside the vitellaria. The testes in the worm from Salvelinus alpinus measured 45-73μ by 45-53μ and are well developed (Plate 4), lying in the medullary regions just inside the vitellaria as before.

The vitellaria (Plate 3 and Plate 4) lie in the cortical zone, but are limited laterally so that none lies in the mid-dorsal or mid-ventral line. They measure 34-72μ by 25-60μ and are normally ovoid. The ovary (Plate 5) is crescent shaped with the horns of the crescent pointing to the dorsal surface and it lies posteriorly to the utero-vaginal aperture. The oviduct

leaves the ovary (Plate 6) in the middle of the concave side and after being joined by the common vitelline duct and the duct from the receptaculum seminis, it enters the ootype before continuing as the proximal end of the uterus. As the uterus leaves the ootype it possesses fairly thick, glandular walls which become gradually thinner until only a thin, membrane-like wall is present where the eggs have shells. In nearly all the worms, the uterus is conspicuous by the presence of large numbers of eggs with shells throughout its many loose coils which occupy almost the whole medullary space between cirrus sacs. The uterus and the vagina open to the outside close together in a common utero-vaginal aperture (Plate 7). The uterine pore is thin-walled while the vagina has a thick muscular wall surrounding the pore and the vaginal duct (Plate 8) as it leads into the centre of the proglottis. There is a slight swelling in the vagina which functions apparently as a receptaculum seminis but this was empty in those worms from Marinogammarus and in those worms recovered from plaice and trout following artificial infestation. In the worms from S. alpinus, however, the receptaculum was more pronounced and contained large numbers of sperm.

The eggs are remarkably constant in size, varying only slightly one way or the other for the longitudinal measurement of 42μ and the diameter of 30μ. In some instances, it appeared that the eggs measured only 40μ by 26μ, but in these cases, it was ascertained that the measurements made were only partial measurements of the whole egg, the measurements having been made from sectioned material.

The longitudinal musculature is not well developed and consists of 150-200 individual muscle fibres which occur either individually or in pairs in the outer cortex, immediately outside the vitellaria. Interspaced between the longitudinal muscle fibres are large parenchymatous cells best seen in the following work with the electron microscope. Although other muscle layers could be distinguished with the electron microscope, as recorded in the work which follows, only the longitudinal muscle layer could be identified with any certainty under the light microscope. Immediately outside the longitudinal muscle fibre layer, is a highly conspicuous tegument or cuticle consisting of two easily distinguished layers (Plate 9). The outer of these consists of a thick layer of hair-like projections, or

microtriches, which are about 4μ long and the inner looks like a homogeneous layer which is also about 4μ in thickness. Both of these layers show to advantage in the electronmicrographs and are discussed further in the following section. Calcareous corpuscles (Plate 10) of various sizes are scattered throughout the cortex but concentrated in large numbers in the region immediately behind the scolex as well as in the scolex. These are also discussed in the following section.

Discussion:

One of the most interesting aspects in the material from Marinogammarus is the complete absence of visible testes and absence of sperm in the receptaculum seminis. This, coupled with the findings that none of the invertebrate hosts could be infested with the eggs taken from these precocious larvae, suggests that the eggs were probably not fertilized despite the fact that they already had shells and were in the uterus.

The fact that testes were seen in a rudimentary condition in the worms recovered from plaice and trout suggests that the definitive host probably provides something essential to testes development and this is further borne out by the fact that fully mature, adult

worms, recovered from Salvelinus alpinus, contained several well-developed testes associated with each group of genitalia. This condition is also found in material identified as Bothrimonus intermedius from Microgadus tomcod which was kindly lent by Dr. W. W. Becklund of the United States National Museum. The fact that both the worms from S. alpinus and also the worms from M. tomcod were smaller than the larval forms from Marinogammarus further suggests that it is the definitive host which is responsible for testes development.

From the above observations it would thus appear that the larval worms found in Marinogammarus are not true neotenic forms as the eggs produced do not seem to be viable. Whether neoteny does exist or not could be established by elucidation of the life cycle and by experimental infestation of the first intermediate host with eggs both from adult worms taken from the definitive host on the one hand and with eggs from precocious larval worms taken from Marinogammarus on the other hand.

Owing to the generous co-operation of the Biological Station of the Fisheries Research Board of Canada in St. Andrews, New Brunswick, this work is now under way.

Ultrastructure of worms from *Marinogammarus pirloti* Sexton and Spooner

Completely surrounding all those worms examined from *M. pirloti*, there is a mucous-like sheath which varies from 1.1μ to 1.4μ in thickness. This is shown in the lower right hand corner of Plate 11 and can be seen at higher magnifications in Plates 12, 14, 15, 16, and 17. This sheath does not appear to be part of the worm itself as there is no limiting membrane around the outside and it probably represents a protective layer secreted by the worm *in situ* in its host. Very little in the way of structure can be seen in this sheath and even at an initial magnification of X40,000 (Plate 17), only small vesicles appear to be present. One of the most interesting features about this sheath is that it disappears following experimental infestation in the definitive host and neither the worms recovered from plaice nor that recovered from the trout show the slightest trace of this sheath.

Lying immediately inside the sheath is the tegument which exists at two levels, a syncytial surface layer of cytoplasm without nuclei which is joined by tubules to an inner layer comprising nucleated areas of cytoplasm between the parenchyma cells. The outer layer

of the tegument is thrown out into a layer of hair-like projections or microtriches which closely resemble the microvilli of the intestine of vertebrates. The microtriches in the present material appear to be longer than those previously described for other species and reach over 4μ long. These can best be seen in longitudinal section in Plate 14.

Each microthrix is made up characteristically of a proximal tubular portion and an electron dense distal portion (Plates 14 and 18). The diameter of the tubular part is about 0.1μ while that of the distal part is slightly less at its base and tapers to a point. Particularly evident in the distal portion of the microtriches (Plate 18) is what appears to be a double membrane the space between the two components being fairly constant at 110-125 Å. The proximal part of each microthrix is clearly continuous with the outer cytoplasmic layer of the tegument and the membrane wall of the microtriches can be seen as a continuation of the outer membrane bounding the tegument (Plate 19). The outer cytoplasmic layer of the tegument appears to be densely granular (Plate 11) but contains several vesicles and is particularly rich in mitochondria in the more proximal part of this layer (Plates 11 and 13). Vesicles of

various sizes can be seen in the outer layer of the tegument and also in between the microtriches (Plates 15, 16, 18, 20, 21, and 22). Sections cut through the scolex also show the same type of structure as was evident in the sections through the strobila of the worm (Plates 23 to 26). Particularly evident, however, in sections through the tegument of the scolex are large vesicles which reach about 2.8μ long by almost 1.3μ in diameter (Plate 23). The greater concentration of excretory vessels in the scolex also may well be associated with the greater activity of this part of the worm.

A continuous series of electron micrographs from the outside of the worm down into the musculature of the scolex can be seen in Plates 23 to 26 and a similar series taken from sections through the strobila can be seen in Plates 27 to 34. The outer tegument does not appear as extensive in the section through the scolex but it is difficult to get an accurate indication as the corresponding sections through the strobila are cut obliquely. In sections through the strobila of the worm recovered following experimental infestation of the trout, however, the width of the outer layer (Plates 39 and 50) is about 4μ which also appears to be the width of the outer layer of the tegument in the scolex of the worm

from Marinogammarus. Accordingly from the evidence available it seems as if this width of 4μ is reasonably constant irrespective of the part of the worm and of the host.

Separating the outer tegumental layer from the series of circular, longitudinal and oblique muscles is a basement membrane easily seen in Plates 24 and 25. The outer tegumental layer, however, projects through this basement membrane where the tegument cells connect to the synicytial layer. These tegument cells which lie scattered between the muscle cells and the parenchyma cells are well characterized by the presence in them of large numbers of mitochondria. The musculature associated with the scolex appears to be much better developed than that of the strobila as does the basement membrane. The series of electron micrographs taken of a section through the strobila (Plates 27 to 34) show that instead of the thick basement membrane present in the previous sections through the scolex (Plates 24 and 25) there is a much more extensive layer consisting of a meshwork of minute fibrils (Plate 30) which is traversed by numerous tubes which probably connect the outer tegument with the tegument cells which lie beneath this fibril layer. The fibrils project deep into the cortex of the worm and are apparently extracellular

structures as they can be seen lying between the various cellular components. (Plates 31, 32, 33, and 34.)

The innermost portions of the tegument cells frequently contain bodies surrounded by several concentric membranes which are exceedingly electron dense (Plates 34, 35, and 36). These lamellated bodies probably correspond to those previously described as phospholipid bodies. The distance between the membranes seems to vary considerably but this is probably due to fixation and sectioning. In plate 36 a well developed body can be seen enclosing what appears to be cytoplasm.

In various sections through the scolex and neck region, large numbers of calcareous corpuscles can be seen (Plates 37, 38, and 39). The osmoregulatory canals have a greatly folded inner surface (Plate 40) and are fed by flame cells which have about 120 cilia closely packed together (Plates 41 and 42) giving the outline of each cilium in cross-section, a six-sided appearance.

Below the level of the tegument cells lie vitelline cells full of yolk droplets (Plates 43, 44, and 45). Each yolk droplet appears to be bounded by a membrane and scattered among the droplets are a few mitochondria.

As was indicated previously (Page 131)

Diplocotyle is a very unusual worm in that eggs with shells are present in larval stages from the intermediate host Marinogammarus. A section through part of the uterus containing eggs shows that each egg (Plate 46) contains several yolk droplets a conspicuous nucleus in which can be seen chromatin material, an endoplasmic reticulum rich in ribosomes, and is surrounded by a relatively thick shell about 1μ across.

Ultrastructure of worms from trout and plaice:

As can be seen in the continuous series of electron micrographs in Plates 47 to 53 the general features of the tegument are extremely similar to those seen in the worms from Marinogammarus. One notable difference, however, is that there is no sheath surrounding the microtriches of the present worm from trout (Plates 47 and 55) whereas there is such a sheath around the worms from Marinogammarus (Plates 11, 12, 14, 15, 16, 17, 20, and 23). Although the microtriches have been cut obliquely in the series shown in Plates 47, 48, and 49, it is still clear that the apical portion of each microthrix is full of an electron dense material whereas the proximal portions are hollow. The outer tegumental layer (Plates 49 and 50) is densely packed with various granules and

other bodies and as before, the mitochondria appear to be concentrated along the inner edge of the outer tegument (Plate 50). The basement membrane is clearly evident (Plates 50 and 51) as is also a connection between the outer tegument and the inner tegument cells. These tegument cells can be seen passing between parenchyma cells (Plates 52 and 53) and are easily recognized by the presence within them of such large numbers of mitochondria. Microtriches of the scolex and neck region can be seen in Plates 54 and 55 and possible evidence of the secretory activity of this region comes from the trail of material seen in both Plates 54 and 55. A large vesicle also appears to have been secreted by the scolex (Plate 55).

Another continuous series of electron micrographs can be seen in Plates 56 to 64. Tegument cells pass between parenchyma cells (Plates 56 and 57) and in Plate 58 the nucleus of one of these tegument cells can be seen with its contained nucleolus. The same cell eventually terminates in the lower left hand corner of Plate 60 and can be seen stretching across Plates 58 and 59, where it contains some of the lamellated bodies described previously. This same area was photographed at lower magnification and is visible in Plate 65. Part of the Golgi apparatus of the same cell can be seen in

Plate 59 and the Golgi apparatus of another tegument cell can be seen in Plate 60. The nucleus of one parenchyma cell can be seen in Plates 60 and 61 and of another in Plate 64. Also present in Plate 64, with a small section on Plate 63, is part of a vitelline cell showing the development of yolk droplets.

As was indicated above, Plate 65 is a photograph of the same area as shown in Plates 58, 59, and 60 taken at lower magnification showing the nucleated tegument cell above, another tegument cell below, and parenchyma cells in between and on both sides. The lamellated bodies mentioned above can be seen well in Plate 66, as can various other inclusions, and the multiple membrane structure of these bodies is clear from the photographs taken at higher magnification and present in plates 67, 68, 69, and 70.

A typical vitelline cell with its yolk droplets, endoplasmic reticulum rich in ribosomes, mitochondria, and nucleus can be seen in Plate 71. The nuclear membrane shows clearly in this cell and several obvious pores through the membrane are present. Granules, apparently similar to the ribosomes, are present within the nucleus but they are not spread throughout, being present only in scattered groups.

Part of the vitelline cell is shown at higher magnification in Plate 72.

In view of the fact that no differences were observed in the electron micrographs of worms recovered from plaice and that from the trout, only a few photographs of particular interest are included of the worms from plaice. What appears to be an early stage in the development of the lamellated bodies previously referred to can be seen in Plate 73 in a tegument cell as well as other bodies at more advanced stages of development.

Various inclusions can also be seen within these bodies in Plates 73, 74, and 75, the last two photographs having been taken at a higher initial magnification. Part of two nuclei of different tegument cells are visible in plates 74 and 75 where the double nuclear membrane and pores connecting the cytoplasm to the nucleoplasm are evident also.

Part of a vitelline cell can be seen in plate 76 enclosing several yolk droplets and in two places can be seen groups of small vesicles not unlike the vesicles associated with the Golgi apparatus, bounded by endoplasmic reticulum devoid of ribosomes.

Discussion:

The ultrastructure of Diplocotyle differs in a number of ways from that of other cestodes investigated. One of the more obvious differences can be seen in the great length of the microtriches of the present material. Those described by Kent (1957) from Hymenolepis diminuta are a little over 0.3μ long; from Raillietina cesticillus are about 0.25μ in length; and from Hymenolepis nana are slightly over 1μ in length. Work done by Béguin (1966) indicates that the microtriches of Caryophyllaeus laticeps are slightly over 0.6μ long and those of Anomotaenia constricta are slightly over 0.5μ long. Finally Threadgold (1965) shows the microtriches of Proteocephalus pollanicoli to be as much as 2.5μ in length but none of these so far described attain a length of 4μ as found in the present material. It is interesting to note that the more primitive worms such as Caryophyllaeus and Proteocephalus along with Diplocotyle tend to have longer microtriches than do the cyclophyllidean worms such as Hymenolepis, Raillietina, and Anomotaenia. The microtriches as described by the authors mentioned appear to lend general support to the idea that cestodes do not possess an outer layer of ectoderm as adults and in reviewing the development of germinal layers of cestodes,

Burt (1963) suggests that the outside layer of adult cestodes is derived from endoderm rather than ectoderm. This view is shared by Schauinsland (1886) who worked on Bothriocephalidae; Vergeer (1936) who worked on Diphyllobothrium latum; and Scott (1965) who worked on Paricterotaenia paradoxa. It would appear, accordingly, that the similarity in structure between the tegument of cestodes and the intestinal epithelium is further reflected both in the similarity of origin and also in the similarity of function as the cestode derives its nutriment by direct absorption through its tegument. It might be worth mentioning that the term tegument has now largely replaced the older term cuticle for the outer structures of cestodes following recent work by Read (1955), Kent (1957), Rothman (1959, 1960, 1963), Threadgold (1962, 1965), and Rosario (1962) who have all shown that this outer layer is not a cuticle in the normal accepted sense of that term but a true cellular tegument.

The nature of the sheath surrounding the tegument of these worms from Marinogammarus is not known, but Monné (1960) indicates that a mucopolysaccharide is secreted by both cestodes and trematodes and that this secretion represents a possible defence mechanism against host enzymes.

Highly evident in the proximal region of the tegument cells in the present material are the lamellated bodies which are probably similar to the phospholipid bodies described by Threadgold (1965). These bodies described by Threadgold, however, do not appear to reach the proportions found in the present material nor does he describe or discuss them further. The function of these bodies is not known but they are very similar in structure to myelinated nerve fibres as described by Ishikawa (1962), Metuzals (1964), and Porter and Bonneville (1964). Despite their similarity, though, it seems unlikely that the present bodies are myelinated nerve fibres in view of the fact that they are intracellular, several apparently being present within a single cell, and also in view of the fact that despite a large number of sections cut in different planes, these bodies always appeared to be in cross-section. This strongly implies that they are more or less spherical and not present as nerve-like fibres.

These lamellated bodies also bear a close resemblance to lamellated inclusion particles described by Dowling and Gibbons (1962) which were seen in the pigment epithelium of albino rats. They compare the lamellated

bodies they found with so called myeloid bodies described in pigment epithelium of various lower vertebrates by Porter and Yamada (1960) and Yamada (1961) but suggest that the structures they describe are different from the myeloid bodies. According to Karli (1954), pigment epithelial cells are capable of ingesting trypan blue particles and are phagocytic and Dowling and Gibbons (1962) suggest that it is the lamellated inclusion bodies which may be responsible for the phagocytic function of the cell. Such an interpretation could also be applied in the present case where the tegument cells, in which these lamellated bodies are found, must be responsible for the intake of nutritional requirements by absorption through the outer tegument. Such absorption may occur by active transfer across the surrounding membrane and also by phagocytosis or pinocytosis.

That the tegument functions in secretion is suggested by the presence of vesicles between the microtriches and it is also considered possible that some vesicles are being absorbed, rather than secreted, due to the function of the tegument, as a whole, in absorption of nutriments.

Smyth (1963,1964) working on *in vitro* cultivation of *Echinococcus granulosus* describes "the secretion of small viscid droplets" by the scolex and he further suggests that these droplets originated in a layer of glandular cells lying just beneath the anterior tip of the rostellum. Although no measurements are given by Smyth, by using the scale given with the photographs it appears that the diameter of these droplets is of the order of 6μ. No mention is made by Smyth of any enclosing membranes around the droplets but it does seem possible that the droplets observed by him being secreted from the scolex of *E. granulosus* may be similar to those secreted by the scolex of *D. nylandica*.

According to Wardle and McLeod (1952), the calcareous corpuscles appear during the development of tapeworms at about the same time as the osmoregulatory system of canals. From the structure of these corpuscles, and in view of the fact that they are concentrated in the scolex and neck region where there is a greater concentration of excretory vessels, it seems likely that they constitute bodies of insoluble metabolic waste products which are laid down in the parenchyma.

The vitelline cells described here have not previously been described from electron microscopic observations and it would be interesting to see whether the compact vitelline gland of cyclophyllidean tapeworms is made up of individual vitelline cells such as are found in the vitellaria of the more primitive Pseudophyllidea exemplified by Diplocotyle.

Within some of the vitelline cells can be seen groups of vesicles not unlike parts of the Golgi apparatus. Although the vesicles are mainly round to slightly oval in cross section without any of the typical elongated sac-like vesicles normally found in the Golgi apparatus their similarity in structure suggests a possible similarity in function.

APPENDIX I

Examination of invertebrates for larval cestodes

Invertebrates collected	Number examined	Larval cestodes looked for	Number of infested invertebrates found
Ants	30	Raillietina	0
Beetles	153	Raillietina	0
Earthworms	1,800	Dilepis	2
		Paricterotaenia	46
Houseflies	32	Choanotaenia	0
Limpets	800	Ophryocotyle	17
Slugs	51	Davainea	0
Snails	8	Davainea	0

APPENDIX II

Experimental infestations using larval cestodes

Species of cestode	Number of larvae used	Experimental host species (number used)	Length of time from infestation to post-mortem examination
Ophryocotyle insignis Lonnberg, 1890	Ca. 10 per host	*Gallus gallus* dom. (4)	24 hr (2 birds) 48 hr (2 birds)
	Ca. 10 per host	*Columba livia* dom. (2)	24 hr (1 bird) 48 hr (1 bird)
	Ca. 10 per host	*Coturnix coturnix* dom. (2)	24 hr (1 bird) 48 hr (1 bird)
	Ca. 10 per host	*Mus musculus* (2)	24 hr (1 mouse) 48 hr (1 mouse)
Paricterotaenia paradoxa (Rudolphi, 1802)	Ca. 100 per host	*Gallus gallus* dom. (4)	24 hr (2 birds) 72 hr (2 birds)
	Ca. 100 per host	*Columba livia* dom. (2)	24 hr (1 bird) 72 hr (1 bird)
	Ca. 100 per host	*Mus musculus* (4)	24 hr (2 mice) 72 hr (2 mice)

Appendix III

Taxonomic position of *Diplocotyle* and *Bothrimonus*

Duvernoy (1842) described a worm, very similar to the present material, under the name of *Bothrimonus sturionis*. This worm had been found by Mr. Lesueur in *Acipenser oxyrhynchus* taken from the Wabasch River in Ohio some years previously. The details of the internal anatomy are not discussed by Duvernoy but he indicates that the scolex possesses a single anterior sucker which has a tendency to form two suckers.

Krabbe (1874) similarly describes a worm very like the present specimens under the name of *Diplocotyle olrikii*. His description is of a worm taken from *Salmo carpio* by Mr. Olrik in Greenland. Once more, the description is mainly of the scolex where the double anterior suckers are mentioned but he states that they are contiguous with each other. In erecting the new genus *Diplocotyle*, Krabbe indicates that its characters place it somewhere between the genera *Ligula* and *Bothriocephalus* but he makes no mention of Duvernoy's work or of *Bothrimonus* and it would appear that he was unaware of the previous description.

Monticelli (1890) describes a new species of *Diplocotyle* under the specific name *rudolphi* to include

worms found in Solea vulgaris and S. impar and the same author (1892) discusses the synonymity of Bothrimonus. In this latter work the following genera are all regarded as synonyms of the genus Bothrimonus Duvernoy, 1842: Bothrimonus Diesing, 1850; Disymphytobothrium Diesing, 1850; Diplocotyle Krabbe, 1874; Cephalocotyleum and Bothriocephalus of Rudolphi (1808-1819).

He recognizes three species as valid and these are: (1) Bothrimonus sturionis Duvernoy, 1842.
(Syn.: Disymphytobothrium paradoxum Diesing, 1854)

(2) Bothrimonus Olrikii Krabbe, 1874.
(Syn.: Diplocotyle Olrikii Krabbe, 1874;
Bothriocephalus carpionis Rudolphi, 1810)

(3) Bothrimonus Rudolphi Monticelli, 1890.
(Syn.: Diplocotyle Rudolphi Monticelli, 1890;
Cephalocotyleum Pleuronectis soleae Rudolphi, 1819)

Lühe (1900) gives a brief diagnosis of the two genera Bothrimonus and Diplocotyle and indicates that they are separated mainly on the structure of the scolex in that they possess either one or two suckers. He also adds another new species to the genus Bothrimonus, namely B. fallax found in Acipenser ruthenus from Rumania.

Schneider (1902), in a major paper on the genus Bothrimonus, states that Diplocotyle is a synonym of Bothrimonus and from personal observations he indicates

that the suckers, which are situated anteriorly on the scolex of these worms, can change drastically in appearance due to the muscular contraction of the scolex so that at times they appear single (which would place them in the genus Bothrimonus) and at other times the same scolices could appear to have double suckers (which would place them in the genus Diplocotyle). Schneider erects a new species, Bothrimonus nylandicus, for worms taken from a flounder and gives an excellent, detailed description of this worm. However, he differentiates this species from other species mainly on the basis of a difference in degree of fusion between the two suckers. This new species appears to fall between B. sturionis Duvernoy and B. rudolphii (Monticelli) being more similar to the latter but Schneider points out that most species are poorly described.

Linstow (1903) does not follow Schneider's lead regarding the synonymity of Diplocotyle and Bothrimonus and erects a further new species in the genus Diplocotyle, namely D. cohaerens from the flat-fish Pleuronectes flesus. He gives an adequate description of his new species but very little in the way of discussion of other species mentioning only D. olrikii Krabbe and D. rudolphii Monticelli.

Spengel (1905) appears to accept Schneider's view that Diplocotyle is synonymous with Bothrimonus as he refers to "Diplocotyle (=Bothrimonus) olrikii" in a general study of several primitive cestodes which are monozoic, i.e. do not show polymorphism in their life cycle.

Levander (1909) records Bothrimonus nylandicus from Pleuronectes flesus and also mentions various items of food which were found in the same host, including the item Gammarus locusta which undoubtedly represents the source of infestation with B. nylandicus.

Cooper (1918) in a major work on the Pseudophyllidea of fishes agrees with Schneider (1902) regarding the synonymity of Diplocotyle with Bothrimonus and under this latter generic name he includes the following as synonyms: Cephalocotylea Diesing, 1850; Disymphytobothrium Diesing, 1854; and Diplocotyle Krabbe, 1874. He redescribes, more fully, the species B. intermedius previously described by him in 1917 and differentiates between this and the following species which are all considered as valid: B. sturionis Duvernoy, 1842; B. olrikii (Krabbe, 1874); B. rudolphii (Monticelli, 1890); B. fallax Lühe, 1900; B. nylandicus Schneider, 1902; B. cohaerens (Linstow, 1903); and B. pachycephalus Linstow, 1904. Diplocotyle serrata

Linstow, 1901 is not considered a valid species of either the genus Diplocotyle or Bothrimonus by Schneider (1902) and this view is also maintained by Cooper. It is interesting to note that the material examined by Cooper and described as Bothrimonus intermedius was found in Pseudopleuronectes americanus from the St. Croix river near St. Andrews, New Brunswick and it is hoped that more material of this worm can be obtained and further work done on the life cycle in the near future.

Nybelin (1922), in a detailed work on the Pseudophyllidea, discusses the genera Diplocotyle, Bothrimonus and Didymobothrium, this latter genus being a new one he creates to include the species rudolphii which was originally described by Monticelli as Diplocotyle Rudolphi. Nybelin redescribes Diplocotyle olrikii and brings it back to the genus Diplocotyle thus not accepting the views of either Schneider or Cooper. He also redescribes Bothrimonus nylandicus Schneider as Diplocotyle nylandica (Schneider) and considers the species cohaerens of Linstow and possibly also the species intermedius of Cooper as synonyms of Schneider's species. The two valid species within the genus Bothrimonus he considers to be sturionis and fallax. Synonymous with B. sturionis is Disymphytobothrium paradoxum Diesing, 1854. Synonymous

with B. fallax are the following: Bothriocephalus punctatus Volz. 1899; Bothrimonus pachycephalus Linstow, 1904 and possibly Bothrimonus caspicus Cholodkowsky, 1915.

Wardle (1932) does not agree with the views of Schneider (1902) or Cooper (1918) but agrees with Nybelin in considering both the genus Diplocotyle and the genus Bothrimonus as valid. He treats all species described on a host basis, thus placing within the genus Bothrimonus those worms found in sturgeon and within the genus Diplocotyle those worms found in Salmonidae. The species found in flat-fish are regarded as similar to those in Salmonidae as Wardle considers the flat-fish to be abnormal hosts for this group of worms. He redescribes Diplocotyle olrikii Krabbe, 1874 and considers both Bothrimonus intermedius and B. nylandicus to be synonymous with this species.

Guiart (1935) briefly describes examples of Diplocotyle olrikii found in Salvelinus salvelinus. Nothing new is added to the description of Diplocotyle olrikii, but Guiart indicates that the following are all synonyms of this worm: Taenia salmonis carpionis Fabricus, 1780; Bothriocephalus carpionis Rudolphi, 1810; Bothriocephalus salmonis umblae Kölliker, 1843; and Bothrimonus olriki Lühe, 1899.

Linton (1941) records Bothrimonus intermedius from several fish hosts collected in the Woods Hole region, Massachusetts. The host species mentioned are: Acanthocottus octodecimspinosus; Microgadus tomcod; Morone americana; and Tautoga onitis.

Doguel and Volkova (1946) describe larval worms found in Gammarus locusta as belonging to the genus Diplocotyle. They state they find it difficult to establish to which species of Diplocotyle their material should be ascribed but consider, as the only two possibilities, D. olrikii and D. nylandica. On ecological grounds, they feel it is more likely that their material represents larval stages of D. nylandica.

Heller (1949) records Diplocotyle olrikii Krabbe, 1874 from Pseudopleuronectes americanus and follows the view of Wardle (1932) that Diplocotyle is essentially a parasite of salmonoid fishes and that flat-fish represent abnormal hosts. Heller found in the worms he examined that "the two bothridial apertures are always distinctly separate" and that his material was similar to that described by Cooper (1917) as Bothrimonus intermedius.

Ronald (1958) records Diplocotyle olrikii Krabbe, 1874 from Hippoglossoides platessoides, Limanda

ferruginea and Pseudopleuronectes americanus but while he refers to Wardle (1932), Ronald does not discuss the synonymity of the worm.

Ouspenskaia (1960) is the second worker to record the plerocercoid of Diplocotyle in a gammarid, the worms in this case being found in Anonyx nugax from the Barents Sea.

Sandeman (1962) also records plerocercoids of Diplocotyle from a gammarid but for the first time in British waters. As indicated in the account of the current work on Diplocotyle, the present material came from the same area as the material collected by Sandeman but the host species appears to be different. The infested gammarids identified by Sandeman belong to the species Marinogammarus finmarchicus whereas the present material has been identified as Marinogammarus pirloti.

Finally, Stark (1965) records Diplocotyle from Gammarus zaddachi in the Yorkshire Esk and although he does not identify to specific level the worms he found, he does indicate that they are similar to D. nylandica (Schneider, 1902). One of the most interesting aspects of the work done by Stark is the indication that of seven different species of gammarids present in the area, only one species was infested with Diplocotyle.

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